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THE RELATIONSHIPS OF THE ARCTOSTYLOPIDAE (MAMMALIA): NEW DATA AND INTERPRETATION

RICHARD L. CIFELLI,[1] CHARLES R. SCHAFF,[2] AND MALCOLM C. McKENNA[3]

CONTENTS

ABSTRACT. The dental morphology of *Arctostylops steini*, hitherto known only from part of the lower cheek-tooth series, is described on the basis of a newly collected specimen including a nearly complete upper and lower dentition. All arctostylopid material from North America, principally from the Clark's Fork Basin, Wyoming, are apparently referable to this single species, which therefore ranges from the late Tiffanian through the Clarkforkian. Other arctostylopid genera are restricted to the Asian Paleogene.

A previously described species of Asian *Palaeostylops* is placed in a new genus *Gashatostylops*. The Arctostylopidae and its constituent subordinate taxa are diagnosed, and a hypothesis of relationships within the family is presented. By comparison with an ungulate morphotype as represented by *Protungulatum*, *Asiostylops spanios* is hypothesized to be the most primitive member of the family. *Bothriostylops notios* and *B. progressus* retain many primitive features but clearly bear some of the specializations seen in *Palaeostylops*, *Arctostylops*, and other advanced genera. Of these derived taxa, North American *Arctostylops* may be the sister taxon to the remaining genera, all of which are Asiatic in distribution. *Anatolostylops* and an as yet unnamed species are highly specialized sister taxa that may be most closely related to *Gashatostylops*.

Comparison of morphotypes for the Arctostylopidae and for southern Notoungulata suggests that derivation of one group from within the other, as presently known, is unlikely. This comparison further indicates that most notoungulate similarities of arctostylopids were independently acquired and that the basis for an exclusive relationship of Arctostylopidae to Notoungulata as sister taxa is a single dental character. The ankles of arctostylopids and notoungulates are divergently specialized and share no characters not present in a eutherian morphotype. The Holarctic family Arctostylopidae is therefore removed from the Notoungulata. Relatives for the Arctostylopidae among Holarctic faunas remain unknown or [illegible], although members of the group resemble certain other enigmatic mammals from the Paleogene of Asia. Because it is a well defined monophyletic unit without obvious close relationship to other mammalian groups, the Arctostylopidae is placed in its own new order, Arctostylopida. Disassociation of the group from the Notoungulata removes the most

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leocene or early Eocene link of Holarctic to Neotropical mammal faunas and suggests, in accordance with other evidence now available, that whatever inter-American connections of mammal faunas occurred must have been earlier in time. The geometry of hypothesized relationships among the Arctostylopidae and the fact that the group was most abundant and diverse in Asia suggest an Asian, rather than North or South American, origin for the family.

INTRODUCTION

Since the studies of Gaudry (1902, 1904, 1906, 1908) and Scott (1904), it has been widely accepted that South America's fauna is largely autochthonous, a result of that continent having been isolated by sea barriers from the rest of the world for most of the Tertiary. Endemism at high taxonomic levels is particularly conspicuous among the land mammals, which underwent their great diversification and radiations largely within the span of the Tertiary. It thus came as a great surprise when, in the first part of this century, apparent members of South America's largest and most characteristic group of hoofed mammals, the Notoungulata, were described from specimens recovered in Wyoming (Matthew, 1915) and Asia (Matthew and Granger, 1925; Matthew, Granger, and Simpson, 1929). Other possible close relatives among Holarctic and Nearctic mammal faunas had been and have continued to be suggested (Ameghino, 1906; Gingerich, 1985; McKenna, 1981). Nonetheless, none of the proposed relationships seemed so certain, based on characteristic synapomorphies, as in the case of these ungulates, for the Holarctic Arctostylopidae possess a strongly specialized dentition that resembles notoungulates alone among mammals. For this reason, the Arctostylopidae have figured prominently in discussions of the origin and early dispersal of South America's native land mammal fauna (McKenna, 1981; Simpson, 1951, 1978, 1980) and of zoogeography in general (Colbert, 1973; Darlington, 1957; Simpson, 1965). In addition, because of their presence in North America and Asia, the Arctostylopidae have been integral to the development of correlations of early Tertiary strata (Dashzeveg, 1982; Gingerich and Rose, 1977; Matthew and Granger, 1925; Szalay and McKenna, 1971).

Arctostylops, represented by the type (and only) species, *A. steini*, was described by Matthew (1915), based on a partial lower jaw from the "lower Gray Bull beds, Clark Fork Basin, Wyoming." This locality is probably, but not certainly, Clarkforkian in age (Rose, 1981). Matthew referred the genus without question to the Notoungulata, hitherto known only from South America, placing it in the "Entelonychia," a mixed assemblage that then contained the most primitive of known notoungulates. Matthew believed *Arctostylops* to be early Eocene in age, which may well be the case, but is a matter of definition. Further materials of the species were not forthcoming for another 50 years, when a specimen was reported nearby from the Silver Coulee beds of the Polecat Bench Formation near Princeton Quarry. This locality is late Paleocene (late Tiffanian) in age (Jepsen and Woodburne, 1969). Intensive collecting by Gingerich, Rose, and associates in Clarkforkian beds of the Clarks Fork Basin has produced four additional specimens, consisting of dentulous lower jaw fragments and isolated teeth (Gingerich and Rose, 1977; Rose, 1981). The single report of *Arctostylops steini* from outside the Clarks Fork Basin is that of McKenna (1980), who recorded the species from beds of Clarkforkian age at Togwotee Pass, northwestern Wyoming.

However, related mammals had in the meantime been recovered from Asia. Paleontological work at Gashato in Mongolia by the American Museum of Natural History's Central Asiatic Expeditions led to the description of two species, *Palaeostylops iturus* Matthew and Granger, 1925 and "*P.*" *macrodon* Matthew, Granger, and Simpson, 1929. These species are probably latest Paleocene in age (Szalay and McKenna, 1971). More recent additions to the group have come from slightly

younger deposits at Naran Bulak, Mongolia (Gradziński et al., 1969), the Paleocene and Eocene (or possibly Oligocene) of China (Tang and Yan, 1976; Zhai, 1978; Zheng, 1979; Zheng and Huang, 1986), and the Paleocene of the USSR (Nesov, 1987), where seven additional described species, placed in six genera, bear witness to a modest radiation of Arctostylopidae in the early Tertiary of Asia.[4] Tang and Yan (1976) described *Sinostylops*, including two species, from the late Paleocene of Anhui Province, China. *S. promissus* (from the Dou-mu Formation), the type species, is based on a mandibular ramus with eight teeth; *S. progressus* (collected in the Shuang-ta-si Group and later transferred to a new genus, *Bothriostylops*) from six jaw fragments. *Anatolostylops dubius* was described by Zhai (1978) from the putative early Eocene (but see below) Shi-san-jian-fang Formation of the Turpan Basin, Xin-jiang Province, China. The species is known from a maxillary fragment with well-preserved M^{2-3}. Two additional genera and species were published by Zheng (1979). *Asiostylops spanios*, from the late Paleocene Lan-ni-kong Member of the Chi-jiang Formation, Jiang-xi Province, China, is based on a skull and associated mandible preserving much of the dentition. Because of its primitiveness with respect to other members of the family, Zheng (1979) placed *Asiostylops* in its own monotypic subfamily. *Allostylops periconatus* Zheng, 1979, from the late Paleocene Wang-wu Member of the Chi-jiang Formation, Jiang-xi Province, is known from an incomplete rostral part of a skull with poorly preserved P^2 to M^3. *Bothriostylops notios*, also from the Wang-wu Member of the Chi-jiang Formation, was described by Zheng and Huang (1986). These authors referred *Sinostylops progressus* to *Bothriostylops*. The most recent addition to the family is *Kazachostylops occidentalis*, described by Nesov (1987) from the late Paleocene Protashkent Svita of Kazakhstan, USSR.

Since the initial descriptions of *Arctostylops* and *Palaeostylops* (Matthew, 1915; Matthew and Granger, 1925), students have realized that these Holarctic forms are, in some respects, more primitive than any known South American Notoungulata, while in other respects they are uniquely specialized. Their primitiveness is reflected by placement of the family Arctostylopidae in Simpson's archaic notoungulate suborder Notioprogonia (Simpson, 1934, 1945). However, the relationships of Holarctic to South American forms have never been considered in detail. For this reason a variety of opinions exist as to the place of origin of notoungulates and their subsequent dispersal patterns, with authors variously favoring northern (Patterson, 1958) or, specifically, Asian (Matthew, 1928; Zheng, 1979); South American (Hoffstetter, 1970; Marshall, de Muizon and Sigé, 1983; Simpson, 1951), and Central American (Gingerich and Rose, 1977) centers of origin.

Until recently, the data base for making such an assessment has been rather limited. The early Tertiary South American notoungulates have received monographic treatment (Simpson, 1948, 1967). The Holarctic radiation, the Arctostylopidae, was long represented only by the single lower dentition originally described for North American *Arctostylops steini* and by dentitions of two species referred to Asian *Palaeostylops*. Although some forms remain poorly known, Asian arctostylopid taxa described in recent years add substantially to knowledge of morphological diversity within the group, offering a dramatically improved basis for comparison with Notoungulata.

Herein we describe the dentition of *Arctostylops steini*, much of which has been hitherto unknown, based on a newly col

[4] An additional, undescribed genus and species has been reported from the late Paleocene Da-tang Member of the Nung-shan Formation, Guang-dong Province, China (Li and Ting, 1983). Dashzeveg (1982) recorded an undescribed species of "*Arctostylops*" from the Bumban Member of the Naran Bulak Formation, Mongolia, higher in the section than the local occurrence of *Palaeostylops iturus*.

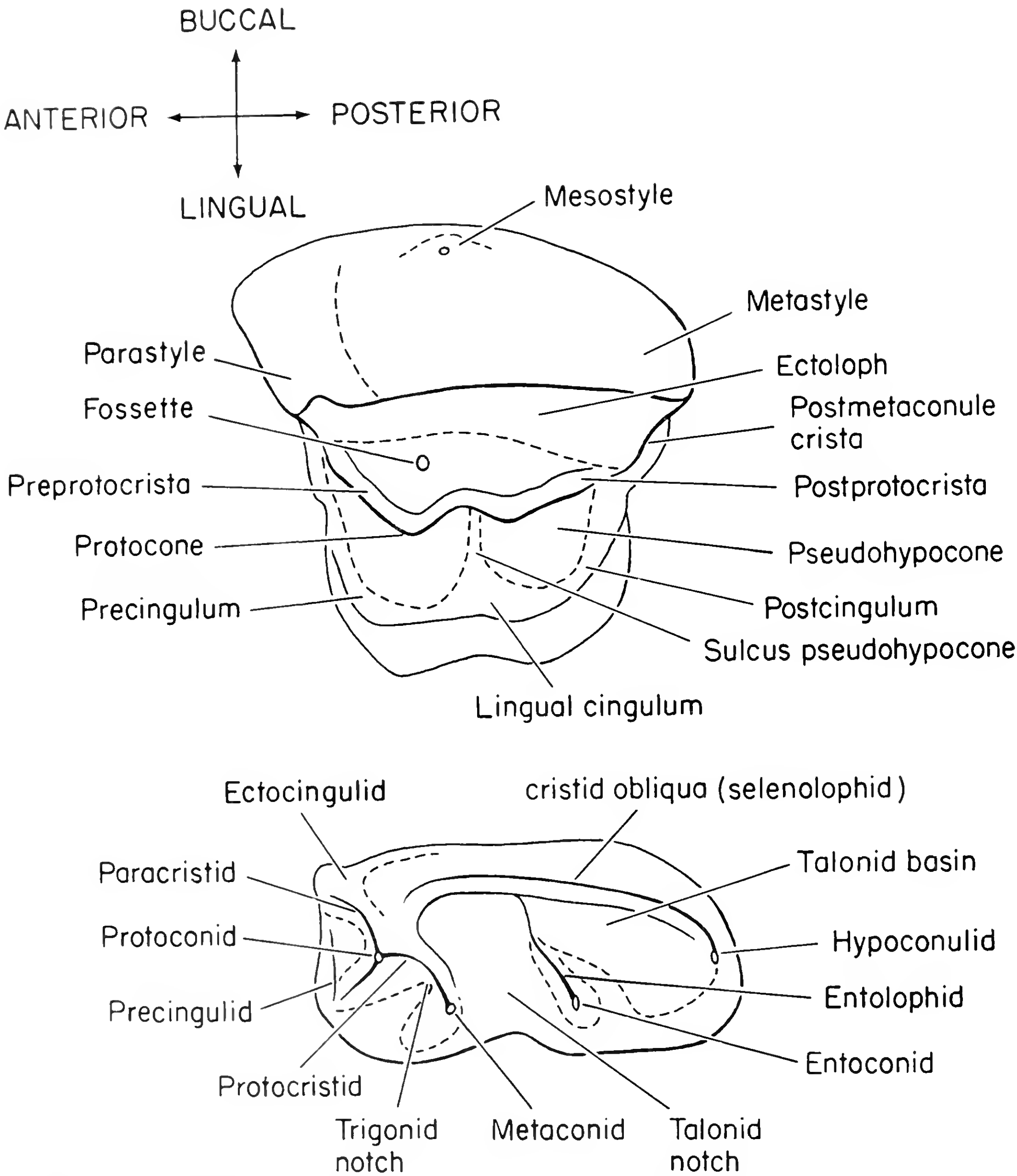

Figure 1 Dental terminology used in describing arctostylopid molars, based on *Palaeostylops iturus* (after Szalay, 1969).

lected and remarkably complete specimen from the late Tiffanian of Wyoming. This specimen forms the basis for a revised diagnosis of the genus and species and for a comparison with Asian Arctostylopidae and South American Notoungulata. Revised diagnoses are presented for previously described taxa; we refer "*Palaeostylops*" *macrodon* to a new genus. Formal description of a hitherto unknown species of arctostylopid from the Yan-ma-tou Formation, Hunan Province, China, is currently

in progress; for comparative purposes, we briefly review some of its morphological features. Another new genus and species, from the Da-Tang Member of the Nung-shan Formation, Guang-dong, is being described by others elsewhere.

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ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; MCZ, Museum of Comparative Zoology, Harvard University; UM, University of Michigan; YPM-PU, Yale Peabody Museum Princeton University Collection.

Dental terminology is illustrated in Figure 1.

SYSTEMATIC PALEONTOLOGY

Order Arctostylopida, new

Distribution. Extinct; presently known only from the Paleocene, Eocene, and possibly the Oligocene of Asia; late Paleocene and possibly early Eocene of North America.

Diagnosis. Small mammals with upper and lower dentitions forming an evenly graded series; canines poorly or not differentiated and without diastemata separating them from adjacent teeth. Posterior upper premolars somewhat molarized except in *Asiostylops*; P^4, at least, with a metacone. Upper molars with well-developed centrocrista, becoming a salient, straight ectoloph in advanced genera; parastyle usually prominent. Pre- and postprotocristae of upper molars strong; conules lacking; upper molars primitively triangular but M^{1-2} becoming quadrate in advanced forms by the addition of a posterolingual cusp (pseudohypocone). Anterior lower premolars serially tricuspid, with strong shearing surfaces; lower molars primitively biselenodont, with paracristid lost and various accessory trigonid structures acquired in advanced taxa. Lower molar hypoconid indistinct, entoconid transversely expanded and, in advanced forms, developed into an anterobucally oriented entolophid.

Family Arctostylopidae Schlosser, 1923, p. 614
(=Subfamily Arctostylopinae Zheng, 1979, p. 391)

Type Genus. Arctostylops Matthew, 1915, p. 429.

Other Included Genera. Anatolostylops Zhai, 1978, p. 109; *Asiostylops* Zheng

1979, p. 388; *Palaeostylops* Matthew and Granger, 1925, p. 2; *Sinostylops* Tang and Yan, 1976, p. 91; *Bothriostylops* Zheng and Huang, 1986, p. 121; *Kazachostylops* Nesov, 1987, p. 212; *Gashatostylops*, new; an unnamed genus; and, with some doubt, *Allostylops* Zheng, 1979, p. 391.

Distribution. Paleocene, Eocene, and possibly the Oligocene of Asia; late Paleocene and possibly early Eocene of North America.

Diagnosis. As for the order.

Zheng (1979) divided the Arctostylopidae into two subfamilies: the Arctostylopinae, which included "typical" genera; and the Asiostylopinae, containing only *Asiostylops* itself. While we are in agreement that this last-named genus is the most primitive of known forms, we choose not to recognize a higher taxon (subfamily) on that basis alone. Moreover, the description of species "intermediate" between *Asiostylops spanios* and advanced forms (see Zheng and Huang, 1986) largely occludes the morphological hiatus distinguishing the proposed subfamilies, so that they are not even clearly defined grades. Nesov (1987) distinguished two further arctostylopid subfamilies, Sinostylopinae and Kazachostylopinae. On the basis of evidence now in hand, we do not believe that such division of the group is warranted.

Arctostylops Matthew, 1915, p. 429

Type Species. Arctostylops steini Matthew, 1915, p. 429.

Included Species. The type only.

Distribution. Late Tiffanian to late Clarkforkian, and possibly Wasatchian, North America.

Diagnosis. Large arctostylopid differing from *Palaeostylops* and all other members of the family in having a salient lingual rib on the lower canine, a molarized P_4 with a low, recurved talonid loph that extends lingually at the posterior margin of the tooth, and a prominent anterolabial cingulum (ectocingulid). Distinct, where known, from primitive genera (*Asiostylops, Bothriostylops*) in having quadrate upper molars with a sulcus separating two lingual cusps on M^{1-2}. Upper molars differ further from those of *Asiostylops* in having a strongly developed ectoloph and in lacking a paracone fold. Lower molars differ from *Asiostylops*, *Kazachostylops*, and *Bothriostylops* in having paracristid reduced, prominent ectocingulid with shear surface descending from protoconid, cristid obliqua achieving a pronounced labial attachment to the trigonid, and entolophid stronger and more oblique. Metacones on P^{2-3} lacking or not so well-developed as in *Palaeostylops* and *Gashatostylops*; a lingual cingulum is present on P^4 and is more salient than in those genera. M^{1-2} more transverse, less quadrate in occlusal view; M^2 sulcus between protocone and pseudohypocone not so well-developed as in *Palaeostylops* or *Gashatostylops*. Metaconid of lower molars not forming a distinct column within the talonid basin as in those two genera. Pre- and postprotocristae of upper molars high and variably enclosing a very transient fossette, as occasionally seen in *Palaeostylops* and *Gashatostylops*, but not so strongly developed as in *Anatolostylops*.

Arctostylops steini Matthew, 1915
Figures 2, 8, 9

Arctostylops steini Matthew, 1915, p. 429; Jepsen and Woodburne, 1969, p. 546; Rose, 1981, p. 96[5]

Holotype. AMNH 16830, left mandibular ramus with P_3 to M_3.

Referred Material. MCZ 20004, associated mandible and anterior part of skull with nearly complete upper and lower dentitions; YPM-PU 20397, poorly pre-

[5] The listing of this species as "*Palaeostylops steini*" by Thenius (1985, caption to Fig. 1, p. 151) deserves mention, although a text explanation is lacking and we are thus uncertain as to whether this is a *lapsus* or implied synonymy. The figure itself is diagrammatic but suggestive of *Palaeostylops iturus* rather than *A. steini* (for which well-preserved upper molars have not been previously reported otherwise). As indicated in the diagnoses, the species are clearly distinct; regardless, *Arctostylops* is the prior name.

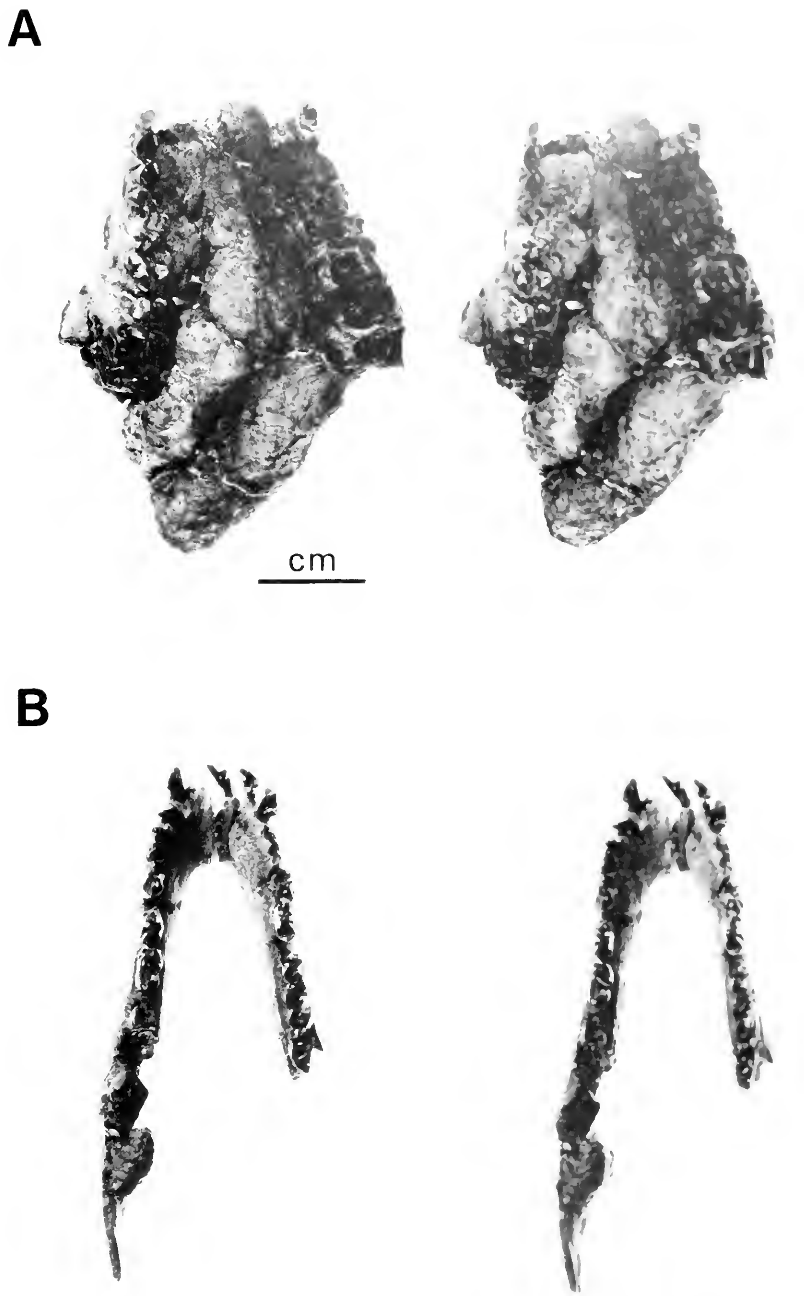


Figure 2. Stereophotographs of upper (A) and lower (B) dentitions of *Arctostylops steini* MCZ 20004

served, incomplete skull and mandible; UM 65024, left dentary fragment with worn M_2, and right dentary fragment with P_3; UM 66707, right dentary fragment with M_1 and partial M_2; UM 68863, right M_2; UM 69280, right P_3 (UM specimens are cited from Rose, 1981, p. 96, and have not been studied by us); and AMNH 88141, trigonid of left M_1.

Horizons and Localities. The type was collected in the "Lower Gray Bull beds, Clark Fork Basin, Wyoming" (Matthew, 1915, p. 429), of probable late Clarkforkian (Rose, 1981) or, possibly, Wasatchian (Jepsen and Woodburne, 1969) age. Referred specimens have been collected from the Willwood Formation at University of Michigan localities SC-19, 116, 188, and 203 in the *Plesiadapis cooki* and *Phenacodus-Ectocion* zones, Clarkforkian, Clarks Fork Basin, Wyoming (Rose, 1981, p. 96); in the "lower variegated sequence" (Love, 1947) of an unnamed formation, Clarkforkian, near Togwotee Pass, Wyoming (McKenna, 1980, p. 330); Silver Coulee beds, Polecat Bench Formation, *Plesiadapis simonsi* zone, Tiffanian (Jepsen and Woodburne, 1969, p. 546), Wyoming. The specimen described below, MCZ 20004, was collected by Charles Schaff and Mark Goodwin in 1977, approximately 5 m from the Princeton Quarry site (Jepsen, 1930). The specimen was excavated from a gray-green siltstone 2.5 m below the Princeton Quarry level. The locality (MCZ number 1/77WYO; SE ¼ sec. 21, T56N, R100W) is about 24 km northwest of Powell, Park Co., Wyoming, on the west side of Polecat Bench.

Diagnosis. As for the genus.

DESCRIPTION

The upper and lower dentitions form evenly graded series, without diastemata or marked structural gaps between teeth. I^1 is not preserved in place in MCZ 20004. However, two isolated upper incisors, one of which has been lost, were found in association with the upper dentition and probably represent this tooth. The crown is mitten-shaped, with a prominent distal heel. A cingulum, lacking on the labial side of the tooth, is well-defined on the lingual portion of the crown. I^2 is represented only by a fragmentary part of the crown. As with the preceding teeth, I^3 is single-rooted. The crests descending from the single cusp are sharp; a small heel is present. A weak labial cingulum is present; a lingual cingulum appears to have been well-developed, but breakage obscures most of this side of the tooth. The upper canine is similar to the incisors and, unlike those of *Palaeostylops* and *Gashatostylops*, which are subequal in size to adjacent teeth, is larger than I^3 and P^1. The single root is round to oval in cross-section and is not well-differentiated from those of the adjacent teeth. The crown bears sharp mesial and distal crests, is labiolingually compressed, and is somewhat inclined posteriorly; the labial surface is convex and the lingual surface is slightly concave. The distal coronal crest bears a small, compressed cusp followed by a faint heel. The cingulum is well-defined both lingually and labially; the posterolabial part bears poorly defined cuspules. There are no diastemata adjacent to the canine.

P^1 is single-rooted and bears a single cusp. The tooth is labiolingually compressed, with a faint lingual bulge, and closely resembles the larger canine. The lingual cingulum is prominent. Salient crests descend from the anterior and posterior ends of the tooth to the single cusp. These evidently were important shearing structures, as a well-defined wear surface is developed on the lingual side of the tooth, obscuring any detail that may originally have been present. P^2, also anteroposteriorly elongate, has two roots and is triangular in coronal view; the serial homologue of the protruding lingual cingulum on P^1 is here developed into a protocone. Labially, the ectoloph is supported by a single prominent cusp, the paracone, from which the loph descends anteriorly and posteriorly. The anterior surface is moderately worn, with the facet angled sharply with respect to the plane of occlusion. This facet is continuous with

TABLE 1. DENTAL MEASUREMENTS [illegible]

	AMNH 16830	MCZ 20004	PU 20397	UM 65024*	[illegible]	[illegible]	[illegible]
A. Lower dentition							
C_1 L	—	—	—				
W	—	—	—	—			
P_1 L	—	1.6	—	—			
W	—	—	—				
P_2 L	—	3.0	—	—			
W	—	1.8	—	—			
P_3 L	3.3	3.4	—	3.6			[illegible]
W	1.7	2.0	—	2.1			[illegible]
P_4 L	3.7	3.8	—	—	—		
W	1.8	2.0	—	—	—		
M_1 L	4.0	4.0	—	3.9	3.7		
W	1.8	2.0	—	2.3	2.3		
M_2 L	4.2	4.7	—	—	—	[illegible]	
W	2.1	2.3	—	—	—	2.2	
M_3 L	3.9	4.5	4.3	—	—	—	
W	1.8	1.9	—	—	—		

	MCZ 20004		PU 20397	
	L	W	L	W
B. Upper dentition				
C^1	3.1	2.0	—	—
P^1	2.9	1.8	—	—
P^2	3.2	2.5	—	—
P^3	3.5	3.3	—	—
P^4	3.6	4.2	—	—
M^1	3.7	4.9	—	—
M^2	4.5	5.6	3.7	4.1
M^3	4.0?	5.1	3.7	4.0

* From Rose (1981, p. 97).

another wear surface that extends from the region of the parastyle to the protocone, along the anterior portion of the lingual cingulum. A faint bulge anterior to the paracone suggests that in the unworn condition a parastyle was present. The part of the ectoloph distal to the paracone bears a strongly developed wear surface, also steeply angled with respect to the occlusal plane. P^3 is larger than P^2, with a better developed protoconal region, more salient paracone fold on the labial surface of the ectoloph, and three roots, but is in most other respects similar to P^2. P^4 bears a well-developed, prominent protocone and is therefore considerably more transverse than P^4. The ectoloph is folded at the paracone. The lingual surface of the ectoloph is considerably worn, but a parastyle and, with less certainty, a metacone may be distinguished. A well-developed crest extends from the protocone to the parastyle. As with P^3, wear on this crest is continuous with that on the anterolingual part of the ectoloph. The remnant of a small fossette persists in the trigon of the right P^4. A well-developed cingulum extends from the parastyle around the base of the protocone and along the posterior border of the tooth. P^4 is nearly the same length as M[illegible]

M^{1-2} are morphologically similar to each other, the principal difference being that M^2 is somewhat larger than M^1; the difference in relative size is less in PU 20397. The ectoloph is anteroposteriorly straight, the only departure from this being the [illegible] salient parastyle, which is developed as a column on the labial wall of the ectoloph.

This ectoloph outer wall also has a posteroinferiorly developed bulge, probably corresponding to the base of a metacone or metastyle. The inner face of the ectoloph on each molar bears a very well-developed wear surface, oriented, as on the premolars, superolingually at a steep angle to the plane of jaw occlusion. A lingual sulcus separates the protocone from another cusp distal and somewhat appressed to it; this latter cusp we believe not to be a true cingulum hypocone, for reasons developed below. The crests linking protocone to parastyle (preprotocrista) and protocone to "pseudohypocone" (Gregory, 1920; Simpson, 1929) to the posterobuccal angle of the tooth (postprotocrista) maintained a primitive triangular arrangement with respect to the ectoloph and were evidently strongly developed, because a small remnant of a fossette enclosed by them persists on the left M^1 and right M^2. These heavily worn crests descend[6] buccally from the protocone to their junction with the descending wear surface of the ectoloph developed on the labial face of the trigon basin, so that the molars appear to be notched when viewed anteroposteriorly. M^3, somewhat damaged on both sides of the specimen, is smaller and more triangular in outline than M^2. An accessory crest, apparently lacking on M^{1-2} but perhaps not seen because of heavy wear on those teeth, sweeps posterolabially from the midpoint of the postprotocrista to the base of the metacone (or metastyle). A small accessory crest, the postmetaconule crista, is present on the left M^3 (the right M^3 is damaged). As with the more anterior molars, a distinct lingual cingulum is present and appears to be confluent around the base of the protocone.

The mandible is shallow and somewhat U-shaped at the symphysis. The symphysis seems to have been unfused. Small mental foramina are located below the right P_4 and below left I_1 and I_2, respectively.

I_1 is not preserved in MCZ 20004. I_2 is procumbent and spatulate, with a long straight root that is round in cross-section. An oblique ridge traverses the lingual surface of the crown. I_3 and the lower canine much resemble I_2, differing in not being procumbent. The canine is thus incisiform, structurally undifferentiated, and not separated from adjacent teeth by diastemata. The crown of C_1 bears a well-developed lingual column; posterior to this, two cuspules, separated by a notch, are present. P_1 is missing as a result of postmortem damage in MCZ 20004 and is represented only by a small remnant of one heel. The tooth was single-rooted. P_2 is a larger tooth and is double-rooted. It is buccolingually compressed and bears three principal cusps that are nearly in line with each other, the middle of which is the tallest. The anteriormost two cusps are separated by a distinct notch; the third cusp lies on the posterior slope of the middle cusp and has been reduced in this specimen by wear. Behind this the central crest slopes inferiorly before rising to a sharp heel at the distal margin of the tooth. A slight bulge is present on the inferolabial side of the tooth, but this is not distinctly formed into a cingulum. P_3 to M_3 are similar to those of the holotype, AMNH 16830, as figured by Matthew (1915). P_3, like P_2, is trenchant and is similar to that tooth except for being larger. P_4 is submolariform. The paraconid is lower than and directly mesial to the protoconid; the metaconid is lingually placed. The protoconid and the metaconid are subequal in size. The cristid obliqua attaches to the trigonid somewhat nearer to the metaconid than to the protoconid and extends superiorly to a level near the apices of these cusps. The talonid is formed by a simple, crescentic crest that terminates at the posterolingual angle of the tooth. A small anterolabial cingulum (ectocingulid) is present.

The lower molars are morphologically

[6] For upper teeth, we follow convention in using the terms "ascend," "descend," "superior," "inferior," and so forth, in a sense relative to the way they are viewed, not with reference to orientation in life.

similar to each other. This series may differ slightly from that of the holotype, AMNH 16830, in that M_2 is more distinctly the largest of the three. The paraconid and its linking crest are altogether lacking, and the protoconid is near the anterolabial margin of the tooth. From this cusp a crest descends anterolabially, forming a distinct ridge (ectocingulid) at that corner of the tooth; the protoconid is also slightly expanded into an anterolingually developed ridge. The cristid obliqua has an extremely labial attachment to the trigonid; i.e., at the protoconid. From this point, at which it is nearly as high as the trigonid, it extends distally as a sharp, straight loph, before curving somewhat lingually to end at the hypoconulid. A hypoconid as such is lacking. The entoconid is transversely developed into a loph (entolophid), which extends anterolabially to join the principal talonid loph (cristid obliqua and postcristid) at about its mid-point. Measurements are given in Table 1.

Available materials of *Arctostylops* are inadequate to properly assess specific variability. All specimens in the hypodigm include teeth also represented in the type of *A. steini* (AMNH 16830) and are sufficiently similar to them in known morphological features to cause us to consider all specimens to belong to the same species. P_3 and M_1 are represented by four specimens each; M_2 and M_3 are known by three teeth each. Of these, M_2 shows a marked variability in length (Table 1). P_3 seems to vary considerably in proportion of length to width, but the significance of this cannot now be determined.

As thus recognized, the species *A. steini* is known from sediments of late Tiffanian (*Plesiadapis simonsi* zone) through Clarkforkian (*Phenacodus-Ectocion* zone) or possibly Wasatchian age. This is a wide stratigraphic range for mammalian species of that age; however, several other species, including the abundant phenacodontids *Phenacodus primaevus*, *P. vortmani* and *Ectocion osbornianus*, are believed to have similar ranges (Rose, 1981, pp. 22–23).

Palaeostylops Matthew and Granger, 1925, p. 2

Type Species. *Palaeostylops iturus* Matthew and Granger, 1925, p. 2.

Included Species. The type only.

Distribution. Late Paleocene to early Eocene (*fide* Li and Ting, 1983), Asia.

Diagnosis. Dentally advanced arctostylopid generally similar to *Arctostylops* but differing in the lack of a heel on [illegible] lack of paracone folds on the ectolophs of P^{3-4}, lack of a lingual rib on C[illegible], and in the lesser size differentiation of the upper canine from adjacent teeth. Molars lower-crowned than in *Anatolostylops*, upper molar fossette more rapidly lost by dental wear. Differs from *Gashatostylops macrodon*, the most closely similar form, in having a strong sulcus separating the lingual cusps of M^1, three upper incisors, and an unconstricted snout, and in lacking cuspules on upper molar lingual cingula and relative enlargement of the upper and lower second molars.

Both *Palaeostylops iturus* and *Gashatostylops macrodon* (herein separated from *Palaeostylops*) were described from the type Gashato Formation (Matthew and Granger 1925; Matthew, Granger, and Simpson, 1929). Both species, but especially *P. iturus*, are known from large samples of rather complete dental materials. Further remains of both species have been recovered in the Naran Bulak Formation by Soviet and Polish-Mongolian expeditions (Gradziński et al., 1969; Szalay and McKenna, 1971) to the Nemegt Valley, about 250 km WSW of Gashato, in the Nomogen Formation, near Nomogen, Nei Mongol, by Chinese workers (Chow et al. 1977; Chow and Qi, 1978), and in the Bayan Ulan Formation, Nei Mongol (Qi, 1979). Individuals of these species represent by far the most abundant members of the Gashato and Nomogen faunas, a curious fact considering the scarcity of their close relative, *Arctostylops*, in nearly contemporaneous North American faunas.

Varied opinions exist as to the status of

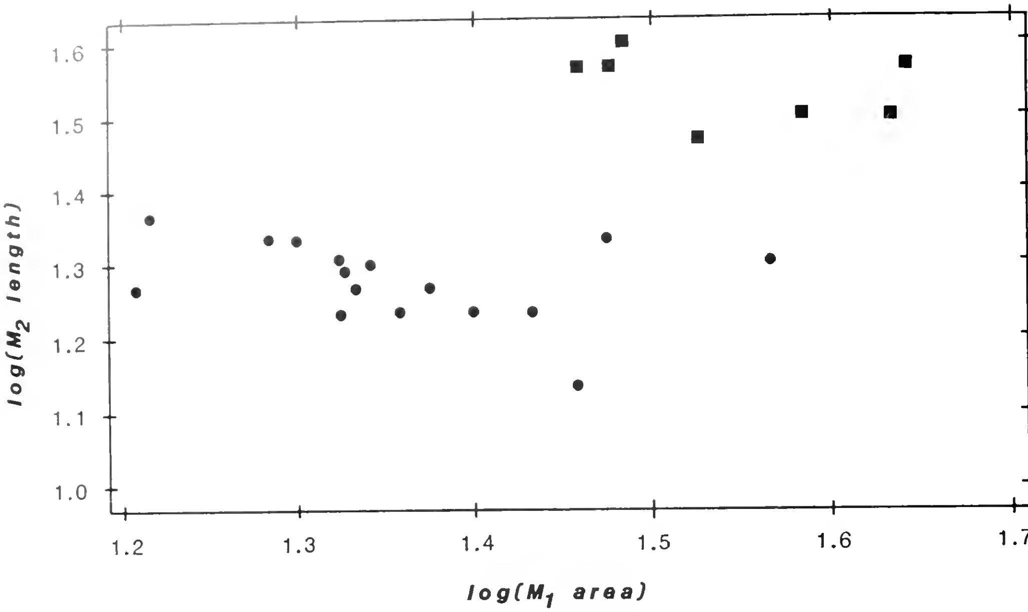
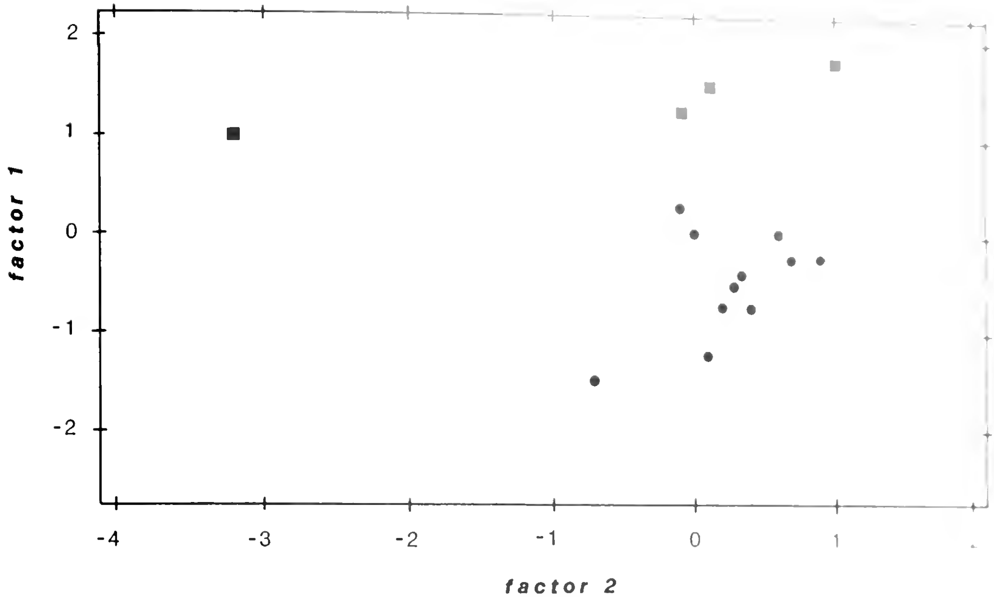


Figure 3. Plot of log-transformed M_1 area vs. M_2 length for *Palaeostylops iturus* (dots) and *Gashatostylops macrodon* (squares).

the genus *Palaeostylops*, its contained species, and the relationships of those species to *Arctostylops steini*. Simpson (1936a) indicated that the species *P. iturus* and "*P.*" *macrodon* might be considered as closely allied but distinct genera; Dashzeveg (1982) referred both to the North American genus *Arctostylops*. The superficially close similarity of the Asian species (except for size) and the fact that they always co-occur suggested to us, at the outset of this study, the possibility that a single, sexually dimorphic, species was represented. Detailed qualitative and quantitative comparisons, presented below, together with previously unknown morphology provided by a new specimen, uphold Simpson's view. To explore the differences between these superficially similar species, we examined available (AMNH) samples of arctostylopid dentitions from the Gashato and Nomogen localities and performed univariate and multivariate analyses on tooth dimension (length, width) data, using the Systat microcomputer software package.

Matthew, Granger, and Simpson (1929) distinguished "*P.*" *macrodon* from *P. iturus* by its larger size and its proportionately larger second upper and lower molars. Comparison of type and referred materials reveal several other consistent morphological differences, summarized in the diagnoses and description given below. The most obvious difference in specimens assigned to the two species, other than absolute size, is the aforementioned disproportionately large upper and lower second molars of "*P.*" *macrodon* (Table 2). Length measurements of these teeth do not even overlap in range, which would be expected if the difference were due to sexual dimorphism. In most mammals (Gingerich, 1974), M_1 is the least variable lower molar; in *Palaeostylops iturus*, the species for which samples are most nearly adequate, variability is comparable between M_1 and M_3 (Table 2). Because M_1 is represented by larger samples in both species, this tooth was chosen as a basis for comparison of second molar proportionate size. A plot (Fig. 3) of log-transformed M_1 area (length × width) against M_2 length indicates that the difference in relative length of the sec-

A



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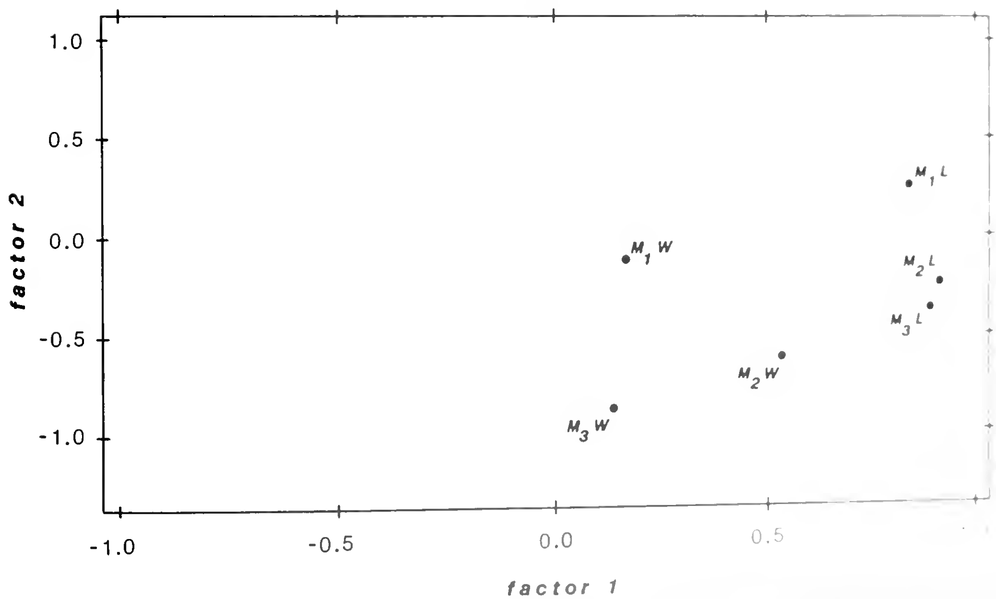

Figure 4. PCA loading plots for six lower molar variables of *Palaeostylops* and *Gas[illegible]* [illegible] on first two axes (dots = *P. iturus*; squares = *G. macrodon*). B. loadings for the six var[illegible]

TABLE 2. MEASUREMENTS AND SUMMARY STATISTICS OF PALAEOSTYLOPS AND GASHATOSTYLOPS (MM; P = P. ITURUS, G = G. MACRODON).

A. Upper cheek teeth

	P^3L		P^3W		P^4L		P^4W		M^1L	
	P	G	P	G	P	G	P	G	P	G
N	2	2	2	2	4	2	3	2	5	5
Minimum	1.880	2.140	1.690	1.850	1.410	2.070	2.210	2.290	2.260	2.670
Maximum	1.990	2.170	1.880	2.000	2.090	2.120	2.320	2.530	2.700	3.220
Mean	1.935	2.155	1.785	1.925	1.812	2.095	2.273	2.410	2.532	2.936
SD	0.078	0.021	0.134	0.106	0.304	0.035	0.057	0.170	0.170	0.210

	M^1W		M^2L		M^2W		M^3L		M^3W	
	P	G	P	G	P	G	P	G	P	G
N	5	5	5	5	4	5	4	3	3	3
Minimum	2.340	2.790	2.670	4.320	3.170	3.630	2.030	1.940	2.570	3.020
Maximum	2.960	3.340	3.560	5.190	3.530	4.100	2.340	2.530	3.060	3.100
Mean	2.772	3.026	3.138	4.788	3.398	3.874	2.135	2.323	2.810	3.063
SD	0.250	0.209	0.328	0.321	0.161	0.177	0.139	0.332	0.245	0.040

B. Lower cheek teeth

	P_3L		P_3W		P_4L		P_4W		M_1L	
	P	G	P	G	P	G	P	G	P	G
N	7	3	7	3	10	4	9	3	16	7
Minimum	1.760	2.090	0.980	1.230	1.960	2.500	1.040	1.300	2.440	2.890
Maximum	2.310	2.370	1.220	1.280	2.500	2.700	1.280	1.440	2.950	3.220
Mean	2.011	2.240	1.164	1.253	2.303	2.612	1.170	1.393	2.737	3.064
SD	0.208	0.141	0.086	0.025	0.153	0.084	0.081	0.081	0.120	0.141
C Var	10.3	—	7.3	—	6.6	—	6.9	—	4.4	—

	M_1W		M_2L		M_2W		M_3L		M_3W	
	P	G	P	G	P	G	P	G	P	G
N	16	7	16	12	16	12	11	4	11	4
Minimum	1.270	1.420	3.060	4.150	1.510	1.750	2.370	3.090	1.330	1.330
Maximum	1.630	1.610	3.850	4.890	2.010	2.550	3.030	3.320	1.520	1.800
Mean	1.425	1.533	3.537	4.592	1.744	2.063	2.694	3.185	1.407	1.505
SD	0.140	0.077	0.194	0.248	0.145	0.248	0.172	0.097	0.060	0.205
C Var	7.3	—	5.5	—	8.3	—	6.4	—	4.3	—

ond molar between the two morphs is not a factor of scaling, i.e., an allometric effect attributable to the fact that "*P.*" *macrodon* is larger than *P. iturus*. Were this the case, all specimens would have fallen along the same line; in the present situation, two lines, with different Y-intercepts, are apparent. To evaluate the significance of differences in measurement means, independent T-tests were performed on the lower cheek-tooth data. For most variables, means of samples assigned to the two species were significantly different at the .05 level (Table 3); probability of identical means was highest for P_3L, P_3W, M_1W, and M_3W and lowest for M_1L, M_2L, M_3L, and M_2W. Principal components analysis, which does not require prior taxonomic sorting, was performed on various combinations of both untransformed and log-transformed lower molar data (the correlation matrix with listwise deletion of missing data and varimax rotation were employed). These analyses consistently separated the specimens into two groups (corresponding to the two species) along the first axis (presumably attributable to size) that, for the untransformed and unrotated lower molar data, accounted for about 61% of the total variance. Factor loading plots (Fig. 4) indicate that the source of this separation is the three length

variables (M_1L, M_2L, M_3L), which have very high loadings along the first axis; a result consistent with the univariate analysis.

Thus, on a statistical basis, the differences between *P. iturus* and "*P.*" *macrodon* are significant and are not attributable to size alone. In addition, dental and cranial features indicate greater structural differences between the species than has hitherto been appreciated. We consider these differences to be worthy of generic separation.

Palaeostylops iturus Matthew and Granger, 1925, p. 2
Arctostylops iturus Dashzeveg and Russell, 1988, p. 131
Figures 7, 8

Holotype. AMNH 20414, right mandibular ramus with broken I_{1-2} and with I_3 to M_3 complete.

Referred Specimens. The type, and the following AMNH specimens, consisting of dentulous upper and lower jaws or portions thereof: 20415, 20417, 22143, 101967, 101968 (uppers); 20429, 21723, 101983, 101985; and AMNH 109522 A–J, casts of 10 uncatalogued lower jaw specimens in the IVPP. The AMNH specimens are from Gashato; the IVPP specimens were collected at Nomogen. Additional materials referable to the species are housed at the Polish Academy of Sciences, Warsaw, and at the Paleontological Institute, Moscow. These specimens are not listed here because we were not able to compare them directly with the fossils listed above.

Horizon and Localities. Late Paleocene; Gashato, Bayan Ulan, Naran Bulak, and Nomogen formations, Nei Mongol.

Diagnosis. As for the genus.

Gashatostylops, new genus

Type Species. Palaeostylops macrodon Matthew, Granger, and Simpson, 1929, p. 11.

Etymology. Gashato-, for the original locality of the type species; -stylops (Gr.), pillarlike, a commonly-used suffix for arctostylopid and primitive notoungulate genera.

TABLE [illegible]. HOMOGENEITY OF GROUP MEANS FOR LOWER CHEEK TOOTH MEASUREMENTS OF *PALAEOSTYLOPS ITURUS* AND *GASHATOSTYLOPS MACRODON*

Variable	*F* Statistic	Prob. identical means
P_3 length	1.711	0.125
P_3 width	1.708	0.126
P_4 length	3.768	0.005
P_4 width	1.110	0.002
M_1 length	5.725	0.000
M_1 width	2.156	0.025
M_2 length	12.650	0.000
M_2 width	4.267	0.000
M_3 length	5.320	0.000
M_3 width	1.501	0.157

Distribution. Late Paleocene to early Eocene (*fide* Li and Ting, 1983), Asia.

Diagnosis. Advanced arctostylopids differing from *Palaeostylops*, the most closely similar genus, in having relatively enlarged upper and lower second molars, in having cuspules, variable in number and development, on the lingual cingula of upper molars; in the weakness or absence of a sulcus separating the lingual cusps of M[illegible], in the presence of two rather than three upper incisors; and in having a laterally constricted snout, with the dental arcade multiply curved. Differs from *Anatolostylops*, to which it may be closely related, in having lower-crowned cheek-teeth and in having upper molars with accessory cusps and plications on the lateral walls of the ectolophs.

Gashatostylops macrodon (Matthew, Granger, and Simpson, 1929)
Palaeostylops macrodon Matthew, Granger, and Simpson, 1929, p. 11
Figures 5–9

Holotype. AMNH 21725, left mandibular ramus with P_3–M_2.

Referred Specimens. The type, an uncatalogued IVPP specimen (casts, AMNH 109521) consisting of the left rostral part of a skull with roots of two right and left incisors, left C–M[illegible], and part of the left mandible with M3, plus an astragalus col

lected by McKenna; AMNH 21742, two isoalted calcanea; AMNH 21726, isolated right astragalus; and the following AMNH specimens consisting of dentulous upper and lower jaw fragments: 22142, 101967, 101979, 101977, 101963 (maxillary); 101980, 101987, 101984, 101982, 101981, 20416, 21740, 21741, 21723, and 21716 (mandibular). The AMNH specimens were collected at Gashato, the IVPP specimen is from Bayan Ulan. As with *Palaeostylops iturus*, additional specimens (not listed here) are in the collections of the Polish Academy of Sciences, Warsaw, and the Paleontological Institute, Moscow.

Horizon and Localities. Late Paleocene; Gashato, Bayan Ulan, Naran Bulak, and Nomogen formations, Nei Mongol.

Diagnosis. As for the genus.

Although a diagnosis appeared in the original publication (Matthew, Granger, and Simpson, 1929), the morphology of this species has never been described. Important details are provided by the specimen represented by AMNH 109521 from Bayan Ulan, which preserves the left side of the rostrum, including the orbit and zygomatic root, left C–M_3, and the roots of the incisors on both sides. In addition, further preparation of the original IVPP specimen by one of us (Schaff) revealed the presence of part of the left mandible, including M_3 and the condyle, and a right astragalus lodged within the broken cranial cavity. These are presumed to be associated with the skull fragment itself. All teeth are in full eruption but wear is light, indicating that the animal was a young adult. The specimen is more or less split sagittally, except that both premaxillae are preserved. The palate, nasal, and frontal regions are crushed, so that the corresponding bones are somewhat fragmented. Comparison with the dentition preserved in original paratypes of the species (AMNH 22144, left P[illegible]–M[illegible]; 22142, right broken M^1 and complete M^{2-3}) and other referred materials from the type locality leave no doubt as to reference of this specimen to *Gashatostylops macrodon*.

As preserved in AMNH 109521, the snout is short and constricted, flaring broadly at the root of the zygomatic arch, so that in palatal aspect the tooth row assumes a double curvature. The form of the dental arcade thus contrasts with that seen in *Palaeostylops iturus*, which curves gently from front to back. In palatal view, the posterior margin of the maxilla forms a curved process that almost completely encloses a small foramen lingual to the junction of M^2 and M^3. This foramen in all probability housed the minor palatine branch of the maxillary artery, as it does in many living mammals and in certain notoungulates, such as *Notopithecus* (see Simpson, 1967, fig. 23). The infraorbital foramen, located above the junction of P^3 and P^4 about halfway between the base of those teeth and the anteroinferior margin of the orbit, is small. The root of the zygomatic arch arises at the base of M^2. It is massive and dorsoventrally expanded, flaring to an inferior prominence at the squamosal suture, suggesting relatively powerful development of the masseteric musculature. The nasals are long and narrow, flaring posteriorly, with the median processes of the frontals deeply projecting between them. Small, isolated foramina are present in each nasal. The premaxillary-maxillary suture is located in the most anterior quarter of the snout, just posterior to I^2. The maxilla is extensive, incorporating three-quarters of the snout region, and extends to the base of the orbit. The maxillary-jugal suture is oblique and runs above the base of M^3.

Although upper incisors are not preserved in the specimen represented by AMNH 109521, roots preserved in the premaxillae clearly indicate that only two were

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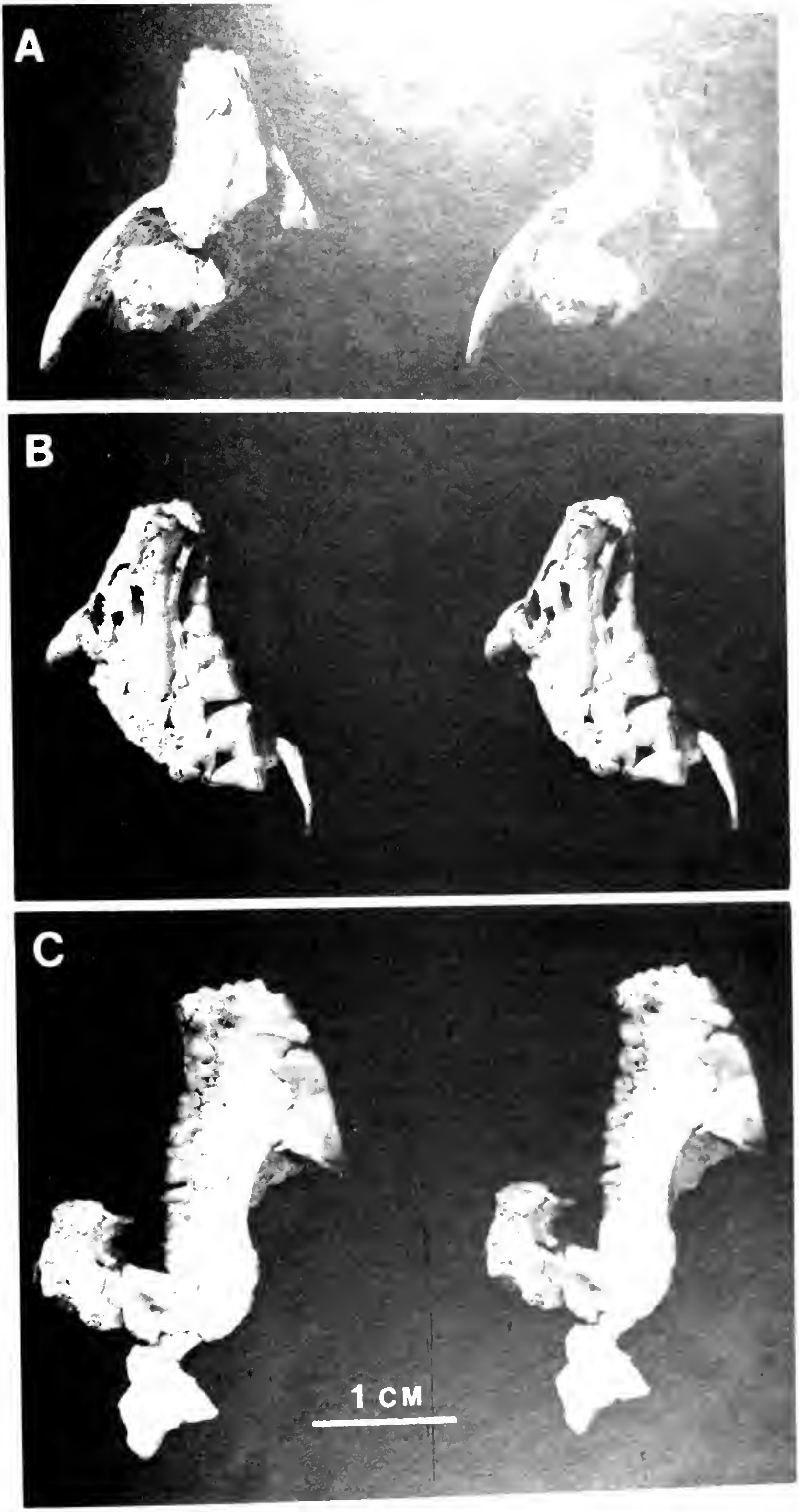
Figure 5. Ster[illegible] [illegible]*atostylops macrodon* and associated partial left mandible (uncatalogued IVPP specimen, cast). A [illegible] and left lateral (C) views.


A
B
C
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present on each side, in contrast to the three known for *Palaeostylops iturus* and *Arctostylops steini*. The roots of both incisors are subround and approximately equal in size. The base of the upper canine is larger than the roots of the incisors, approximating the base of P^1 in size. Whether or not this reflects a notable difference in size between canine and lateral incisor crowns cannot be determined; however, root development is comparable in *Palaeostylops iturus*, whose anterior teeth nonetheless form an evenly graded series (cf. Matthew, Granger, and Simpson, 1929, p. 12). P^1 is single-rooted. Its crown, generally similar to those of corresponding teeth in *Palaeostylops* and *Arctostylops*, is buccolingually compressed and bears a sharp mesiodistal crest, which ascends medially to the apex of the single cusp. A faint lingual cingulum, not developed into a heel as in *Palaeostylops*, is present. P^2 is double-rooted. It is larger than P^1 and structurally similar to it, except that a protocone, smaller than that of *Arctostylops* and equal to that of *Palaeostylops*, is developed lingually. Well-defined crests descend from this cusp to the anterior and posterior margins of the tooth. The lingual surface of the coronal crest, or ectoloph, is steep and bears well-marked wear facets, as seen in succeeding teeth. P^{3-4} are successively larger and more molariform, with more fully developed protocones. As in *Palaeostylops iturus* but in contrast to *Arctostylops steini*, P^4 is noticeably smaller than M^1. The molars bear sharp, straight ectolophs with well-developed parastyles. On M^1, the lingual sulcus posterior to the protocone is faint, unlike the condition seen in *Palaeostylops*. Lingual cingula are well-developed on all upper molars; cusps, variable in development, are present on M^{1-2}. M^1 in the specimen represented by AMNH 109521 bears two such cusps, one lingual to the protocone and another, larger, posterolingual to that cusp and in a hypoconal position. M^2 is much larger than preceding or succeeding teeth and bears three cusps on the lingual cingulum. Posterior to the protocone the lingual sulcus is strong, so that the tooth is bilobed. A prominent accessory cusp lies in a median position at the base of the ectoloph, posterior to the parastyle. M^3 is generally similar to those of *Arctostylops steini* and *Palaeostylops iturus*, except that the lingual cingulum is complete and bears an eminence directly lingual to the protocone.

A nearly complete lower dentition is represented in AMNH 21741 from Gashato, a left dentary with I_{1-3}, C, P_{1-4}, and M_{1-3}; the last molar bears a moderately damaged talonid. The horizontal ramus is shallow, with a nearly horizontal symphysis that appears to have been unfused. Small foramina are located below P_1 and P_4. The three incisors are similar to those of *Palaeostylops iturus*. I_1 is spatulate with a rounded point and a median vertical ridge, the crown being less compressed than in *Arctostylops steini*. I_2 is larger and more laterally compressed than I_1, with the anterior part of the crown more expanded and the median vertical ridge better developed. I_3 is similar in size and morphology to I_2, except for the presence of an incipient posterior lobe on the median ridge. The canine is subequal in size to I_3 and somewhat larger than P_1; no diastemata separate it from those teeth. The crown of the canine is tricuspid and compressed; lingual crests are associated with each cusp. In these respects it generally resembles *Palaeostylops iturus* rather than *Arctostylops steini*.

The single-rooted P_1 is morphologically similar to the canine, although the three coronal cusps are somewhat more distinct. P_2 is double-rooted and significantly larger than P_1, with the tricuspid pattern clearly defined. P_3 is similar to but larger than P_2, with the protoconid being the tallest cusp. P_4 is submolariform, with a serially tricuspid trigonid and a small, crested heel. The paraconid and metaconid are equal in size, and the protoconid is the tallest cusp. The cristid obliqua attaches somewhat labial to the metaconid. There is no ectocingulid present on any of the lower premolars.

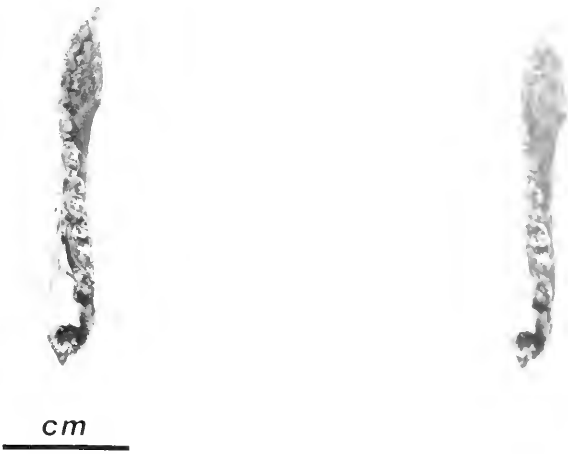


Figure 6. Stereophotographs of left mandible of *Gashatostylops macrodon*, AMNH 21741

The most notable feature of the lower molars is the extremely salient, blade-like, labially-placed cristid obliqua. The molars are morphologically similar to each other, with M_2 appearing to be disproportionately larger than preceding and succeeding teeth. The entoconid is expanded into an obliquely-oriented entolophid that contacts the cristid obliqua in about the middle of the talonid. On all three molars, the ectocingulid is developed as a distinct anterolingual ridge at the junction of protoconid and cristid obliqua. The protoconid is the tallest cusp except on M_2, in which the hypoconulid is larger.

No directly associated, articulated postcranial elements are yet known for any of the Arctostylopidae, but proximal ankle bones may now be referred to *Palaeostylops iturus* and *Gashatostylops macrodon* with little doubt. These species are by a considerable margin the most abundant taxa known from Gashato. Isolated astragali and calcanea, of appropriate size for *P. iturus* and *G. macrodon*, occur there in the same relative abundances as dental remains of these species. Furthermore, an astragalus was found lodged within the cranial cavity of a specimen from Bayan Ulan referred to *G. macrodon* (see below). This astragalus, for which association is reasonably inferred, resembles to the point of identity the isolated specimens from Gashato believed on the basis of size and relative abundance to belong to *Gashatostylops macrodon*. In known respects the ankle of *Palaeostylops iturus* is similar to that of *G. macrodon*, and it is therefore not described separately. Descriptive terminology follows that of Cifelli (1983b). Relative terms in the description are based on comparison with ankle bones referred to *Protungulatum* and similar taxa, which are assumed to approximate a eutherian morphotype (Szalay and Decker, 1974; Szalay, 1977).

As represented by AMNH 21726, a right astragalus from Gashato, the astragalar body is mediolaterally compressed, with nearly vertical sides; there is little or no development of a fibular shelf on the lateral side. The body is more or less cylindrical, with the tibial trochlea marked by a median groove and well-defined, raised borders. An astragalar foramen is apparently lacking; a pit is present on the tibial trochlea of AMNH 21726, but appears to have been caused by diagenetic corrosion of the fossil (as on the other side of the same specimen; such pitting is common on fossils from Gashato). The neck is of moderate length but is notably constricted, so

that the head is clearly demarcated. The head itself is subround with, however, the navicular facet developed as a flattened band that does not extend onto its sides. The navicular facet extends far superiorly, onto the dorsal side of the bone, and is developed so that movement between astragalus and navicular would have been subparallel rather than highly oblique to that between astragalus and tibia. There is no observable separate facet for the cuboid. The tarsus might thus tentatively be regarded as "serial" (see discussion by Osborn, 1889), although this cannot be definitively ascertained until a well-preserved, articulated foot is discovered. The sustentacular facet is unremarkable, except that it is somewhat larger and better developed distally than it is in *Protungulatum*. The ectal facet is very steeply inclined, and the interarticular sulcus separating the two facets is deep.

The calcaneus, as represented by AMNH 21742 (complete left calcaneus and right calcaneus lacking the tuber, almost certainly not from the same individual), is notable in having a short neck (that part anterior to the astragalocalcaneal facets) relative to the tuber. The ectal prominence is dominated by a very strongly developed fibular facet, which forms a broad, anteroposteriorly oriented, semicylindrical surface. Medial to this lies the ectal facet, which is strongly inclined with respect to the fibular facet. The sustentaculum is unusual in lying at or near the distal end of the bone; a prominent "beak" is developed on the superior distomedial corner of the bone. The cuboid facet is developed at a moderate angle with respect to the long axis of the calcaneus. Comparisons to other taxa are deferred until the discussion.

Sinostylops Tang and Yan, 1976, p. 91

Type Species. Sinostylops promissus Tang and Yan, 1976, p. 92.

Included Species. The type only.

Distribution. Late Paleocene (*fide* Li and Ting, 1983). Asia.

Diagnosis. Primitive arctostylopids differing from *Asiostylops* in having higher-crowned molars and a metaconid on $P_{?3}$. Distinct from advanced genera such as *Arctostylops* in retaining a paracristid on the lower molars. Similar to *Bothriostylops* in having the cristid obliqua attaching to the trigonid of lower molars in a lingual position, but differs from that genus in having higher-crowned molars and a more slender, elongate P_3.

Sinostylops promissus Tang and Yan, 1976, p. 92

Holotype. IVPP V4263, right mandibular ramus with eight partial or complete teeth.

Hypodigm. The type only.

Horizon and Locality. IVPP locality 71017, Dou-mu Formation, Anhui Province, People's Republic of China; late Paleocene.

Diagnosis. As for the genus.

With the removal of referred species "*Sinostylops*" *progressus* to *Bothriostylops*, the concept and affinities of *Sinostylops* become problematic. The identities of the eight teeth in the holotype and only specimen of *Sinostylops promissus* are open to doubt. Because the third from the last tooth is remarkably low-crowned and long, unlike either preceding or succeeding teeth, we believe it to be deciduous. The penultimate tooth, although much smaller than the ultimate, is morphologically similar to it; both are badly damaged but apparently were bicrescentic, which is not the case for the more anterior teeth. We therefore believe the teeth in this specimen to be I_3–P_3, dP_4, and M_{1-2}, although other interpretations are possible. Available materials of *Sinostylops promissus* and *Bothriostylops progressus* suggest further differences between the species beyond those listed in the diagnoses, but because of the uncertain identities of the teeth in IVPP 4263 and because of postmortem damage to that specimen, we are unable to evaluate the significance of these differences.

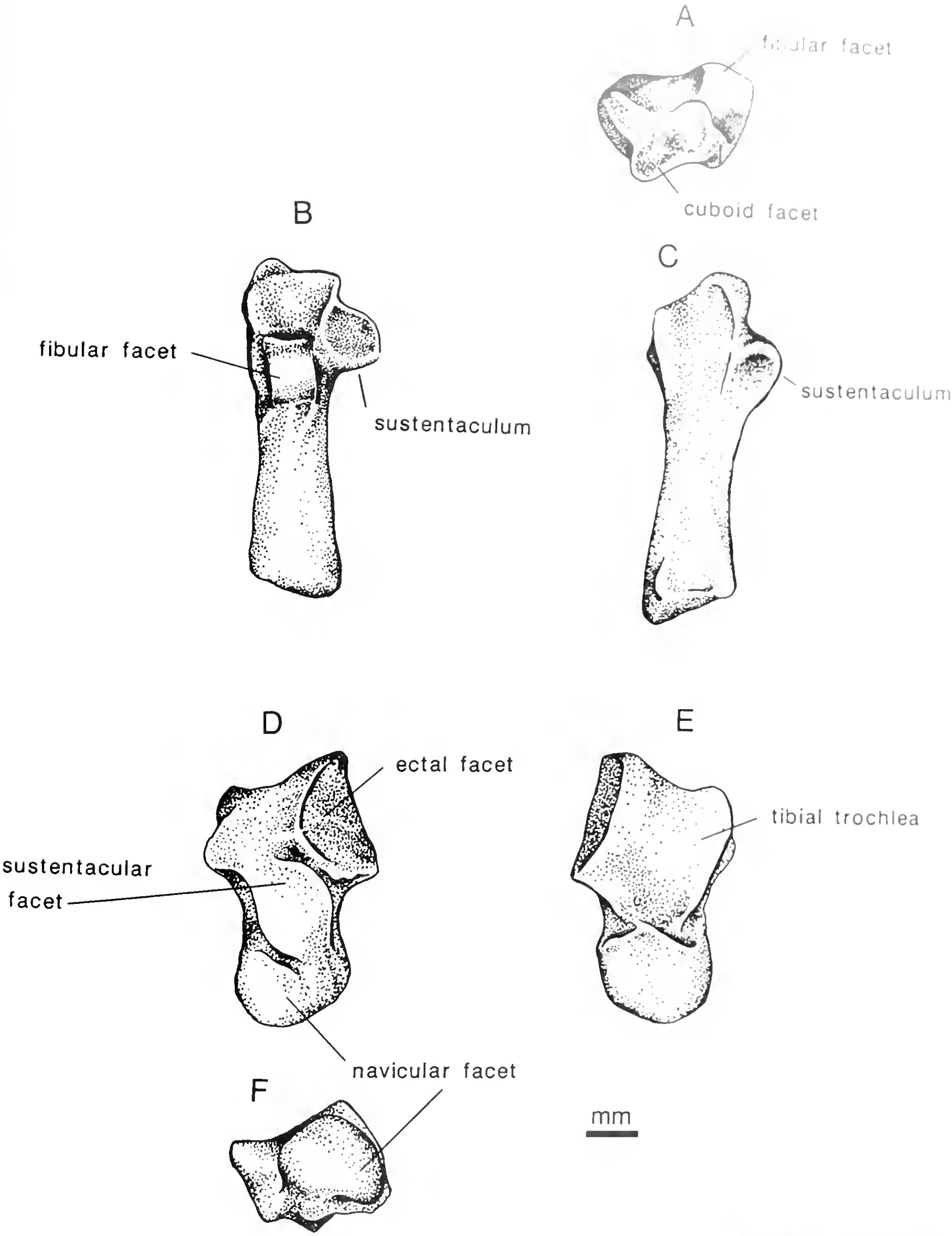


Figure 7. Right astragalus (unnumbered IVPP specimen associated with rostrum of skull, a cast of which is numbered AMNH 109521) and left calcaneus (AMNH 21742) of *Gashatostylops macrodon*. A, B, C: calcaneus in distal, dorsal, and planter views, respectively; D, E, F: astragalus in plantar, dorsal, and distal views, respectively

Bothriostylops Zheng and Huang, 1986, p. 121

Type Species. Bothriostylops notios Zheng and Huang, 1986, p. 122.

Referred Species. The type, and *Bothriostylops progressus* (Tang and Yan, 1976, p. 92).

Distribution. Late Paleocene, Asia.

Diagnosis. Primitive arctostylopids with brachydont teeth, differing from *Asiostylops*, which they generally resemble, in having a crescentic P_4 talonid; and from all known genera in having M_3 with an elongate talonid, the hypoconulid forming a distinct lobe.

A number of other characters were listed in the diagnosis and description of the genus (Zheng and Huang, 1986). Of these, the presence of a deep median labial groove and convex labial wall on lower molars were cited as important similarities to *Asiostylops*. We see no distinction of arctostylopid genera on this basis but, lacking access to the original specimens (especially the type of *Bothriostylops notios*), we defer to Zheng and Huang (1986). Nonetheless, we observe that a deep median external groove is present on lower molars of *Sinostylops promissus*. Even on the basis of the single, enigmatic specimen available, it is clear that this latter species is rather divergent and not obviously congeneric with other known taxa.

Bothriostylops notios Zheng and Huang, 1986, p. 122

Holotype. IVPP V7642, portion of left mandible with P_4–M_3.

Referred Specimens. The type only.

Horizon and Locality. Wang-wu Member, Chi-jiang Formation; late Paleocene. North of Zhulin Hill, Dayu County, Jiangxi Province, People's Republic of China (cited from Zheng and Huang, 1986).

Diagnosis. Cheek-teeth lower-crowned than in *B. progressus*. Entolophid of lower molars not so well-developed as in that species and, at least on M_3, incomplete; trigonid of lower molars more open lingually, with the paracristid less truncated, than in *B. progressus*.

Bothriostylops progressus (Tang and Yan, 1976)

Figures 8, 9

Sinostylops progressus Tang and Yan, 1976, p. 92

Bothriostylops progressus Zheng and Huang, 1986, p. 127

Holotype. IVPP V4264.1, fragment of right mandibular ramus with M_2.

Referred Specimens. The type, and IVPP 4264.2, right mandible fragment with worn M_{2-3}; 4264.3, right mandible fragment with P_{3-4}; 4264.4, right mandible fragment with P_{3-4}; 4264.5, right mandible fragment with M_2 and with broken M_3; 4264.6, right maxillary fragment with broken M^1 and with M^{2-3} well-worn.

Horizon and Locality. IVPP locality 71071, Shuang-ta-si Group, Anhui Province, People's Republic of China; late Paleocene (Li and Ting, 1983) or early Eocene (Zheng and Huang, 1986).

Diagnosis. Cheek-teeth higher-crowned than in *B. notios*. Entolophid of lower molars complete and more fully developed than in that species; trigonid of lower molars more compressed, with paracristid more truncated, than in *B. notios*.

Anatolostylops Zhai, 1978, p. 109

Anatostylops, Schaff, 1985, p. 593

Type Species. Anatolostylops dubius Zhai, 1978, p. 109.

Included Species. The type only.

Distribution. Late early Eocene or early middle Eocene (*fide* Li and Ting, 1983) or, perhaps, Oligocene (*fide* Zhai, personal communication); Asia.

Diagnosis. Differs from all other genera, excepting an unnamed form, in having higher-crowned cheek-teeth; ectoloph of upper molars elongate, smooth and featureless, with a large parastyle but no parastylar fold. Pre- and postprotocristae salient, enclosing a fossette that persists through more advanced wear than in other forms. Sulcus on lingual side of M^2 crown

not so broad as in *Arctostylops* or *Palaeostylops*. Differs from a closely similar unnamed genus and species in having a lingual division of M^2, and in lacking the great anteroposterior expansion of the ectoloph and the strong development of the postcingulum seen on upper molars of that genus.

Anatolostylops dubius Zhai, 1978, p. 109
Figure 8

Holotype. IVPP V4357, fragment of left maxilla with M^{2-3}.

Hypodigm. The type only.

Horizon and Locality. Shi-san-jian-fang Formation, Turpan Basin, Xin-jiang Province, People's Republic of China; Eocene or Oligocene (see above).

Diagnosis. As for the genus.

Asiostylops Zheng, 1979, p. 388

Type Species. Asiostylops spanios Zheng, 1979, p. 388

Included Species. The type only.

Distribution. Late Paleocene (*fide* Li and Ting, 1983), Asia.

Diagnosis. Distinct from all other arctostylopid genera in the more transverse P^{2-3}, with a lesser development of the protoconal region; upper molars lacking a posterolingual cusp or other secondary coronal complications; metaconid lacking on P_3. Lower molars primitive in retaining the paracristid, as in *Bothriostylops* and *Sinostylops* but not other genera; cristid obliqua attaching to trigonid in a median position. Entolophid feebly developed and transversely oriented.

Asiostylops spanios Zheng, 1979, p. 388
Figures 8, 9

Holotype. IVPP V5042, cranium and associated left mandible.

Hypodigm. The type only.

Horizon and Locality. IVPP locality 73039, Lan-ni-kong Member, Chi-jiang Formation, Jiang-xi Province, People's Republic of China.

Diagnosis. As for the genus.

Kazachostylops Nesov, 1987, p. 212

Type Species. Kazachostylops occidentalis Nesov, 1987, p. 212

Included Species. The type only

Distribution. Late Paleocene, western Asia.

Diagnosis (from Nesov 1987, p. 211) Small arctostylopids with long, tall paracristid on lower molars; premetacristid and postmetacristid reduced to absent. Entolophid of M_{2-3} long, nearly transverse, and joined with the talonid loph. Crests of molar teeth form practically uninterrupted cutting edges.

Lacking access to the two, relatively good specimens of the type and only species of *Kazachostylops*, we defer to Nesov's brief diagnosis of the genus, and omit it from the detailed comparisons and discussion presented below. From the figures, *Kazachostylops* appears to be rather similar to *Bothriostylops* and, perhaps, *Sinostylops*, particularly in the elongate, well-developed M_3, the strong, crescentic paracristid, and in the lingual attachment of cristid obliqua to trigonid (i.e., at the metaconid).

Kazachostylops occidentalis Nesov, 1987, p. 212

Holotype. Specimen number 10 12455, indicated by Nesov (1987) as being deposited in the Ts N E G R Museum, Kazakhstan, Dzhilga, USSR, consisting of a right dentary with C, P_{3-4}, and M_1.

Hypodigm. The type, and at least one more dentulous jaw fragment figured by Nesov (1987), number 12 12455, consisting of a right maxilla with P^2 to M

Horizon and Locality. Marginal marine deposits of the Pretashkent Svita, late Paleocene; site TDA-2, Kazakhstan, Dzhilga, USSR (*fide* Nesov, 1987, p. 212)

Diagnosis. As for the genus

Arctostylopidae?, incertae sedis
Allostylops Zheng, 1979, p. 391

Type Species. Allostylops periconatus Zheng, 1979, p. 391

Included Species. The type only

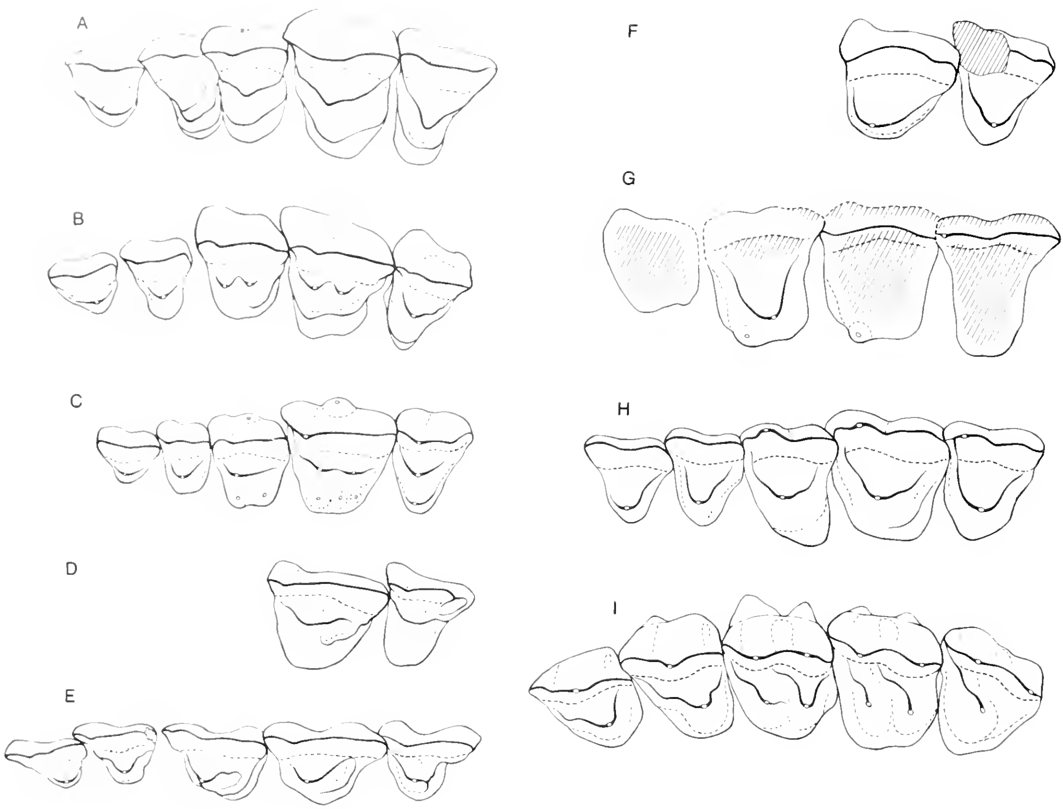


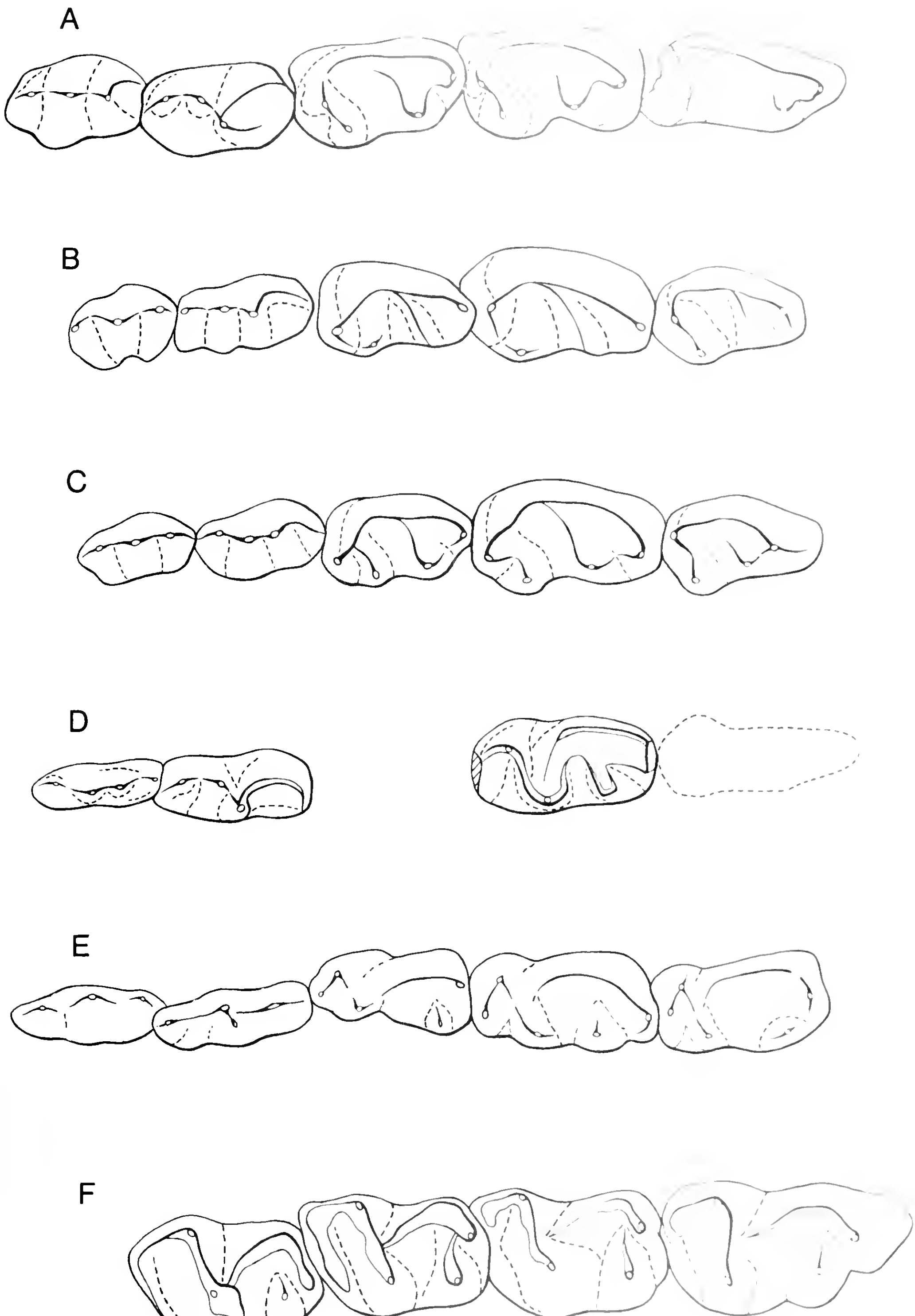
Figure 8. Comparative series of arctostylopid (A–H) and primitive notoungulate (I) upper dentitions. Teeth standardized to size and reversed where necessary. A, *Arctostylops steini* (MCZ 20004); B, *Palaeostylops iturus* (AMNH 22143); C, *Gashatostylops macrodon* (cast, AMNH 109521); D, *Anatolostylops dibius* (IVPP V4357); E, undescribed genus and species (unnumbered IVPP specimen); F, *Bothriostylops progressus* (IVPP V4264.6); G, *Allostylops periconatus* (IVPP V5043); H, *Asiostylops spanios* (IVPP V5042); I, *Peripantostylops minutus* (AMNH 28494).

Distribution. Late Paleocene (*fide* Li and Ting, 1983), Asia.

Diagnosis. Generally primitive ?arctostylopids similar to *Asiostylops spanios* in the low-crowned cheek-teeth, the small size of P^3, and the presence of a paracone fold on the ectoloph of at least some upper molars, but differing from that species in having a hypocone on M^2. Differs from advanced arctostylopids (*Palaeostylops, Arctostylops, Gashatostylops, Anatolostylops*) in having lower-crowned cheek-teeth, a smaller P^3, smaller upper molar parastyles, and a broadly expanded posterior cingulum on M^1. *Allostylops* is distinct from all forms in the family save

→

Figure 9. Comparative series of arctostylopid (A–E) and primitive notoungulate (F) lower dentitions. Teeth standardized to size and reversed where necessary. A, *Arctostylops steini* (MCZ 20004); B, *Palaeostylops iturus* (AMNH 20414); C, *Gashatostylops macrodon* (AMNH 21741); D, *Bothriostylops progressus* (P_{3-4}, IVPP V4264.4; M_2, IVPP V4264.1; M_3 outline, IVPP V4264.2); E, *Asiostylops spanios* (IVPP V5042); F, *Peripantostylops minutus* (AMNH 28494).


A
B
C
D
E
F

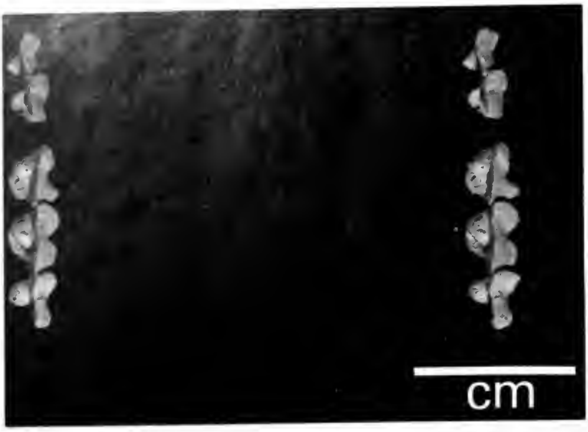


Figure 10. Stereophotographs of P^3–M^3 of undescribed genus and species of Arctostylopidae (unnumbered IVPP specimen).

Gashatostylops in having a prominent pericone anterolingual to the protocone on upper molars.

Allostylops periconatus Zheng, 1979, p. 391

Holotype. IVPP V5043, badly preserved rostral portion of cranium.

Hypodigm. The type only.

Horizon and Locality. IVPP locality 73041, Wang-wu Member, Chi-Jiang Formation, Jiang-xi Province, People's Republic of China; late Paleocene.

Diagnosis. As for the genus.

Arctostylopidae, genus and species indet. A

In addition to the foregoing previously described species, an unnamed arctostylopid is represented by an upper dentition collected from the Yan-ma-tou Formation, Hunan Province, People's Republic of China. While full description of this species is in progress, we briefly note some of its morphological features here in order to facilitate comparison among other members of the family and to aid in assessing their relationships.

The taxon in question is a small, dentally advanced arctostylopid similar to *Anatolostylops* in having high-crowned cheek-teeth and a smooth ectoloph on the upper molars, but it differs from this and all other genera in the great anteroposterior expansion of the ectoloph crest on P^3–M^3 and in the strong development of the postcingulum on M^{1-2}. Indeed, the ectolophs of the upper cheek-teeth are so strongly developed that the rest of each tooth appears by comparison to have been constructed as an afterthought. A lingual division of M^{1-2}, seen in all other genera except *Asiostylops*, is lacking. The second upper molar is notably larger than the first.

The single specimen representing this species was plotted into a measured section (Unit 21 of Zhu-chen, 1986) of beds reported to be of Cretaceous age. The basis for this surprising age determination is not entirely clear, but it seems to involve fossil remains believed to be dinosaur eggs (listed as *Elongatoolithus* and other taxa) which, apparently, bracket the arctostylopid specimen. Other fossils from this section are listed merely as "animal bones" or "animal teeth," and are therefore of little help in age determination. However, a mammalian axis vertebra is larger than that of any Chinese Paleocene mammal and would be totally out of place in the Cretaceous, as would a large anterior tooth of some ungulate-sized mammal. We believe on this basis that the locality is much younger than Cretaceous, perhaps even Eocene in age, whether dinosaurs were present or not. Indeed, the advanced mor-

phology of the small, distinctive arctostylopid from this site is suggestive of the Eocene or possibly Oligocene *Anatolostylops dubius*.

Arctostylopidae, genus and species indet. B

Another arctostylopid, which we have not seen, occurs in the late Paleocene Datang Member of the Nung-shan Formation, Nan-xiong basin, Guang-dong, People's Republic of China. The animal is regarded as a new genus and species by Li and Ting (1983, p. 13).

COMPARATIVE DENTAL MORPHOLOGY OF THE ARCTOSTYLOPIDAE

Review of dental variations among the Arctostylopidae and assessment of the relative primitiveness of various character states is based on comparison with an ungulate morphotype as represented by *Protungulatum* and various comparable oxyclaenine Arctocyonidae (Cifelli, 1983a). Some of the features that are represented in available materials of the known species are summarized in Table 4. The most primitive arctostylopid for which good materials are available is unquestionably *Asiostylops spanios* Zheng, 1979. Zheng (1979) referred *Asiostylops* to the Notoungulata based on the biselenodont lower molars, with shortened trigonid and lophodont entoconid, and on the upper molar ectoloph, with parastyle developed. He considered *Asiostylops* to be primitive within the order because the cheek-teeth are low-crowned, the premolars are not molarized (in particular, P_4 lacks an entoconid), the lower molars have a pronounced paraconid, and the upper molars lack the secondary coronal complications seen in *Henricosbornia* and more advanced South American notoungulates.

Compared to an ungulate morphotype represented by *Protungulatum*, *Asiostylops spanios* has a greater development of the protocone on P^{3-4}, with a metacone on those teeth; upper molars with an ectoloph (strong, high centrocrista connecting paracone and metacone), strong, complete lingual cingula, indistinct conules and reduced stylar prominences, blade-like serially tricuspidate P , with notches separating the cusps; P_4 with a trigonid crest that is slightly curved (metaconid lingually placed) and a straight, short talonid crest, lower molars with a crescentic trigonid, paraconid in a median position, and a talonid consisting of cristid obliqua and postcristid united into a continuous crescent with hypoconid and hypoconulid indistinct. The entoconid of lower molars is isolated from the posteristid and developed into a faint, transverse loph which extends anterolabially to the talonid crescent. Many of these features are shared by presumably unrelated groups of mammals, but the serially tricuspid anterior lower premolars and the transversely developed entoconid (entolophid) of the lower molars are rather distinctive characters.

Arctostylops, *Palaeostylops*, and *Gashatostylops* are distinctively more specialized. Advanced characters of these three genera with respect to *Asiostylops* include higher-crowned posterior premolars and molars; an expanded protocone on P^3; upper molars with a high, flat ectoloph wall including parastylar and metastylar folds only (*Asiostylops* has a distinct paracone fold); M^2, at least, is bifid lingually, with high pre- and postprotocristae that enclose a very transient trigon fossette but which are rapidly reduced by heavy wear. The lower molars of these three genera are distinctive in a number of respects, such as: 1) the presence of a salient, pillar-like, ectocingulid with a wear surface descending along its face; 2) the reduction of the trigonid by loss of the paracristid; 3) the presence of a high, shearing talonid crescent (cristid obliqua), which joins the trigonid labial to position of the protoconid, and 4) the strongly developed, oblique entolophid. All three genera have an anteriorly placed P_4 paraconid, unlike *Asiostylops*. The polarities of some features of P_4 are uncertain. *Arctostylops* differs from

Palaeostylops, *Gashatostylops*, and most other Arctostylopidae in the presence of a crescentic P_4 talonid loph, and differs from *Gashatostylops macrodon* (but not *Palaeostylops iturus* and several other species) in the lingual placement of its P_4 metaconid. *Arctostylops steini* is probably autapomorphous in having a stronger ectocingulid on P_{3-4}, a stronger lingual rib on C_1, a prominent heel on I^1, and a slightly larger protocone on P^2. *Palaeostylops* and *Gashatostylops* appear to be derived with respect to *Arctostylops* in the lesser differentiation of C^1, the lack of paracone folds on the ectolophs of P^{3-4}, and the presence of a shearing notch on P_4. *Palaeostylops* and *Gashatostylops* differ from *Arctostylops* also in the more quadrate, less transverse nature of M^{1-2} and in the fact that the sulcus between the two internal cusps is better developed, at least on M^1. The P_4 cusps in *Gashatostylops macrodon* are more or less anteroposteriorly aligned, as with the more anterior premolars of all genera; the talonid crest is a straight, bladelike structure. *G. macrodon* is also distinctive in that the upper and lower second molars are greatly enlarged, in the variable development of one or more cuspules on the lingual cingulum, and in the reduction or absence of a lingual suclus on M^1 (further distinctions are given in the diagnoses provided above). Thus, *Arctostylops*, *Gashatostylops*, and *Palaeostylops* share presumed synapomorphies with respect to *Asiostylops*. Within this clade of advanced genera, there is some evidence to suggest that *Gashatostylops* and *Palaeostylops* shared a more recent common ancestor than either did with *Arctostylops*. Because of uncertainty in morphocline of several features, the possibility of lineal relationships between any of the included species cannot be evaluated.

The remaining species of Arctostylopidae are known from less complete materials and there is, accordingly, some uncertainty as to various character states. Although rather primitive, the two species of *Bothriostylops* are unique among arctostylopids in having an elongate M_3 in which the hypoconulid forms a separate lobe. (This also appears to be true of lower molars belonging to *Kazachostylops occidentalis*, which we have not examined firsthand. We are unable to consider the species further here, but note that the above-mentioned feature and several other lower molar characters suggest a close relationship to *Bothriostylops* spp.) We assume, for the purpose of comparison, that these two species form an exclusive unit within the family. Thus conceived, *Bothriostylops* is, in several respects, intermediate beteen *Asiostylops* on the one hand and advanced arctostylopids (*Arctostylops*, *Gashatostylops*, *Palaeostylops*) on the other. As in *Asiostylops*, *Palaeostylops*, and *Arctostylops*, the metaconid on P_4 is lingually placed (we are uncertain of the condition in *B. notios*). The talonid crest of that tooth is curved in *Bothriostylops* spp, although not so strongly as in *Arctostylops*. The lower molar trigonids of *B. progressus* are anteroposteriorly compressed, as in the derived genera, but unlike those forms, part of the paracristid remains, as in *Asiostylops*. In *B. notios*, the trigonid retains a more open arrangement, with the paracristid little reduced. The cristid obliqua attaches to the trigonid at a lingual position, near the apex of the metaconid, unlike either *Asiostylops* on the one hand or *Palaeostylops*/*Arctostylops* on the other. The ectocingulid is feebly developed and not expanded into an occlusal structure. The entolophid varies from well-developed (*B. progressus*), as in the advanced forms, to weak and incomplete (*B. notios*). A partial, very worn, upper molar series is available for *Bothriostylops progressus*, but it adds little to knowledge of the species. The ectoloph appears to have been high; as far as can be determined, paracone and metastylar folds are lacking although a parastylar fold is well-developed. M^1 has a sulcus separating two lingual cusps; this appears not to have been true of M^2, which is triangular in outline (as with *Asiostylops*), but excessive wear has obscured de-

TABLE 4. DENTAL CHARACTER COMPARISONS AMONG THE ARCTOSTYLOPIDAE.

Character	*Asio. spanios*	*Sino. promissus*	*Bothrio. notios*	*Bothrio. progressus*	*Arcto. steini*	*Palaeo. iturus*	*Gashato. macrodon*	*Anatol. dubius*	Undescr. Taxon
P_3 metaconid	absent	present	?	present	present	present	present	?	?
P_4 metaconid	lingual	?	lingual	lingual	lingual	lingual	lingual	?	?
P_4 talonid	straight	?	curved	curved	curved	shearing notch	shearing notch	?	?
P. paraconid	lingual	?	?	lingual	labial	labial	labial	?	?
P. ectocingulid	absent	?	?	faint	strong	faint	faint	?	?
M ectocingulid	absent	present	present	present	pillar	pillar	pillar	?	?
M cr. obliqua	medial	lingual	lingual	lingual	labial	labial	labial	?	?
M entolophid	weak/abs.	?	weak/abs.	strong	strong	strong	strong	?	?
M paracristid	present	present	present	present	absent	absent	absent	?	?
M_3 hyld lobe	absent	?	present	present	absent	absent	absent	?	?
Enlarged M2	absent	absent	absent	absent	absent	absent	present	present	present
Crown height	low	moderate	moderate	moderate	high	high	high	v. high	v. high
P^{3-4} pa fold	present	?	?	?	present	absent	absent	?	absent
M pa fold	present	?	?	absent	absent	absent	absent	absent	absent
M parastyle	small	?	?	large	large	large	large	v. large	v. large
M pas fold	present	?	?	present	present	present	present	absent	absent
M ling. sulcus	absent	?	?	M^1	M^{1-2}	M^{1-2}	M^2, sm. M^1	?, M^2	absent
M^{1-2} cingulum	incomplete	?	?	complete	complete	complete	complete	complete	complete
M ectoloph	low	?	?	high	high	high	high	high, long	high, long
M protocristae	weak	?	?	?	strong	strong	strong	v. strong	v. strong

tails of crown morphology. M^2 may have been slightly larger than the adjacent teeth, but it is not greatly enlarged as in *Gashatostylops macrodon*.

As for *Sinostylops promissus* Tang and Yan, 1976, poor preservation of the type and only known specimen leaves various character states open to question. It cannot be determined if an entolophid was present on M_{1-2}. It appears that a trigonid crescent was retained, as in *Asiostylops*, and the cristid obliqua attaches to the trigonid at the metaconid, as in *Bothriostylops* spp. The antemolariform teeth form a graded series and are long, narrow, and bladelike, especially dP_4. The premolars are serially tricuspid, with a straight, crested heel. *Sinostylops promissus* lacks advanced features of the lower molars seen in *Palaeostylops* and *Arctostylops*. The morphology of the premolars would seem to indicate pertinence to the Arctostylopidae; within the family, *Sinostylops promissus* is similar only to *Bothriostylops* spp in the lingual attachment of cristid obliqua to trigonid.

Allostylops periconatus Zheng, 1979, about which little can be said, is represented by the rostral part of a skull with the dentition very poorly preserved. The upper molars resemble those of *Asiostylops*, and are therefore presumably primitive, in lacking an enlarged parastyle and in retaining paracone and metacone folds on the ectoloph. There was, apparently, no posterointernal cusp on M^{1-2}; a prominent anterolingual cusp (pericone) is present on the lingual cingulum, as is variably present on upper molars of *Gashatostylops macrodon*. The posterior cingulum of M^{1-2} is broadly expanded, so that the molars are subquadrate in occlusal aspect. The dentition as preserved gives little indication of affinity to this group, and the position of *Allostylops* is therefore indeterminate.

Anatolostylops dubius Zhai, 1978, known from M^{2-3}, is clearly a rather specialized form and may be significantly younger than the other genera. As in *Palaeostylops*, *Arctostylops*, *Gashatostylops*, and *Bothriostylops*, the ectoloph is high and lacks a paracone fold; unlike those forms, the ectoloph is otherwise featureless, lacking a parastylar fold or basal bulges in the regions of parastyle and metastyle. The lingual coronal crests (pre- and postprotocristae) are strong and enclose a fossette that probably persists into a fairly advanced stage of wear. The sulcus between the lingual cusps on M^2 is not so deep as in *Palaeostylops* or *Gashatostylops* but, as in those genera, it probably persists to advanced wear. A lingual cingulum is weak or lacking on M^3, as in *Bothriostylops progressus*; as in *Gashatostylops macrodon*, M^2 is considerably larger than M^3. *Anatolostylops* is most closely similar to the unnamed genus and species, with which it shares several derived characters not found in other Arctostylopidae. The ectoloph is anteroposteriorly elongate, with labial plications reduced or lost. The lingual division of upper molars is poorly marked in *Anatolostylops* and absent in the unnamed form; because these genera otherwise appear to be closely related to forms in which it is well-developed (e.g., *Palaeostylops*), we believe this to represent reduction or loss rather than retention of a primitive condition (as in *Asiostylops*). The cheek-teeth of the undescribed genus and *Anatolostylops* are higher-crowned than in other genera, and the pre- and postprotocristae better developed, enclosing a more persistent fossette than in other members of the family. Although *Gashatostylops* is autapomorphous in several respects, notably in the development of accessory cuspules on the lingual cingulum and base of the ectoloph of upper molars, it is similar to *Anatolostylops* and the undescribed form in several other respects. These include a reduction of the lingual sulcus on at least the first tooth of the upper molar series and the great size of the second molar relative to that of adjacent teeth.

Among advanced Arctostylopidae, *Anatolostylops* is divergent in having double opposition of upper to lower teeth, as indicated by the presence of a distinct wear facet in the mesostylar area of the upper molar (this would correspond to a facet

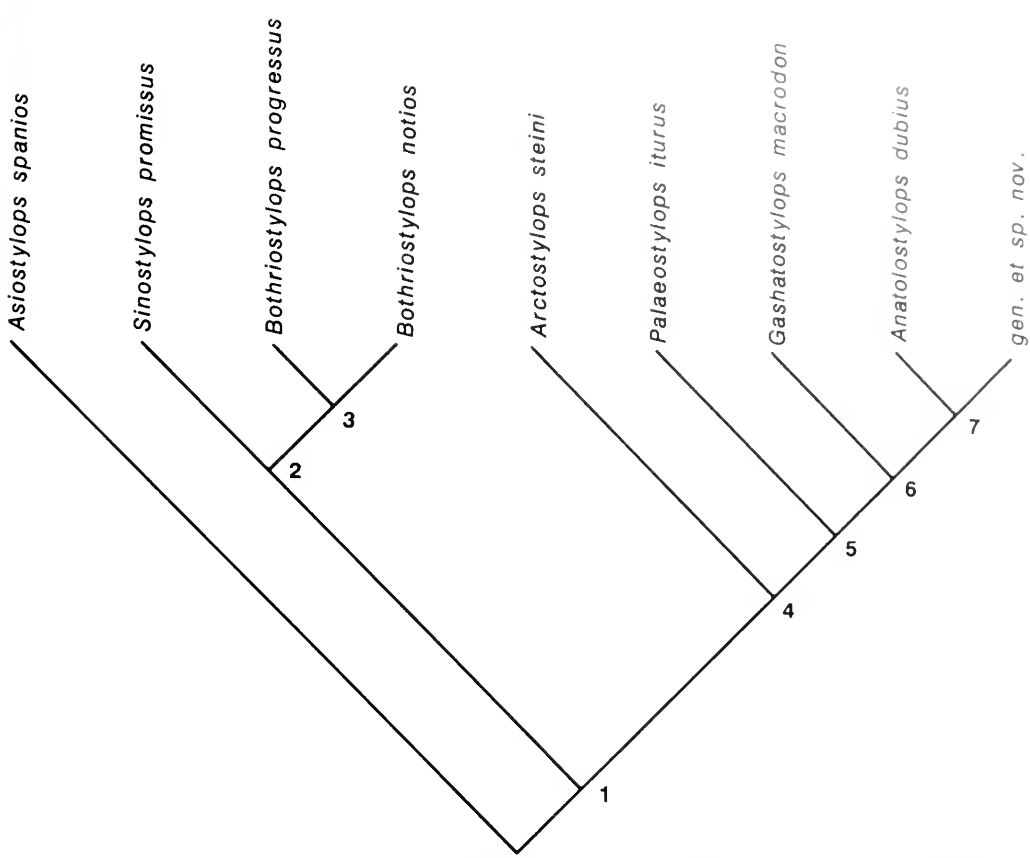


Figure 11. Hypothesized relationships among the Arctostylopidae. Characters at nodes (see Table 4): 1) metaconid added to P_3, pseudohypocone on at least one upper molar, upper molar paracone fold lost, ectocingulid developed on lower molars, ectocingulid developed on P_4, P_4 talonid curved, upper molar parastyle enlarged; 2) lower molar cristid obliqua attaches lingually to rear of trigonid; 3) M_3 elongate? (condition unknown in *S. promissus*); 4) lower molar entolophid well developed, lower molar cristid obliqua attaches labially to rear of trigonid, lower molar ectocingulid strong and pillarlike, P_4 paraconid shifted labially lower molar paracristid lost; 5) shearing notch developed on P_4 talonid, P^{3-4} paracone fold lost, canines lesser differentiated, 6) second molars enlarged, pseudohypocone lost on M^1?; 7) upper molar protocristae salient, M^2 pseudohypocone reduced?, parastyle fold on ectoloph of posterior upper cheek teeth lost, ectoloph of upper molars anteroposteriorly elongate, cheek teeth very high crowned.

anterior to the protoconid on the lower molars, which are not known for *Anatolostylops*). This facet is lacking in *Arctostylops*, *Palaeostylops*, and *Gashatostylops*, which apparently had singly opposing upper and lower cheek teeth.

An hypothesis of interrelationships of the Arctostylopidae is given in Figure 11[7] (*Kazachostylops occidentalis*, which we have not examined first-hand, and *Allostylops periconatus*, poorly known and of doubtful affinities, have been omitted from this phylogeny). *Asiostylops spanios* is the most primitive taxon known and is considered to represent the sister group of all remaining taxa. *Bothriostylops* spp., unique in at least one character (the presence of a hypoconulid lobe on M_3), generally resemble *Asiostylops* in their retention of primitive features, but nonetheless appear to share several derived features with the remaining taxa. Among these are the presence of a P_3 metaconid, a curved P_4 talonid, a lingual division of M , and the loss of the

[7] The absence of a chronologic dimension is due to uncertainties of relative age, not our lack of appreciation for this consideration.

paracone fold and the presence of a large parastyle on the upper molars. *Sinostylops promissus* (poorly known and lacking much of the most diagnostic morphology in the type and only specimen) is similar only to *Bothriostylops* spp in its lingual cristid obliqua-trigonid attachment; it is very tentatively regarded as the sister taxon of *Bothriostylops* spp. The remaining Arctostylopidae clearly are united by derived morphology not found in *Asiostylops* or *Bothriostylops*. These features include mainly specializations of the lower cheekteeth, such as the labial attachment of the cristid obliqua, the presence of a pillar-like ectocingulid, and the loss of the paracristid. Among advanced genera, *Arctostylops* appears to be the most primitive, lacking specializations such as a shearing notch on P_4, found in *Palaeostylops* and *Gashatostylops*. Within the group formed by the remaining genera, the undescribed form and *Anatolostylops* possess several synapomorphies (mainly features related to the hypertrophied ectoloph of upper molars) and both share with *Gashatostylops* an enlarged second molar.

THE NOTOUNGULATA OF SOUTH AMERICA

The early Tertiary Notoungulata of South America have been fully reviewed by Simpson (1948, 1967). Additions to knowledge since publication of these monographs have been principally the Itaboraian to Casamayoran notoungulates of Itaboraí, Brazil (Paula Couto, 1952, 1954, 1978) and of northwestern Argentina (Bond, 1981; Pascual, Vucetich, and Fernandez, 1978; Vucetich, 1980). As recognized by Simpson, the major advanced notoungulate suborders Toxodonta and Typotheria (including Hegetotheria; see Cifelli, 1985a) were differentiated by the late Paleocene, with 5 families collectively represented. Simpson grouped two other families of the earliest faunas (Riochican and Casamayoran), the Henricosborniidae and Notostylopidae, into his paraphyletic suborder Notioprogonia. When compared with an ungulate morphotype, of which *Protungulatum* is a good approximation, all these notoungulates of the earliest faunas share a number of dental specializations (Figs. 8I, 9F). The posterior upper premolars (P^{3-4}) are somewhat molarized, with large protocones supporting anterior and posterior lingual cingula and trigonal crests; the teeth are dominated labially by a prominent paracone, which is separated from the also well-developed parastyle and metastyle. A metacone, as far as is known, does not develop on upper premolars of notoungulates. Illustrated specimens of *Henricosbornia lophodonta* (Simpson, 1948, figure 53) and *Oldfieldthomasia debilitata* (Simpson, 1967, plate 5) have metacones on the teeth indicated to be P^4, but comparison with other materials belonging to these species indicate that the teeth in question are probably deciduous. The upper molars bear a strong ectoloph whose labial wall is marked by sulci separating parastyle, paracone, and metacone. M^{1-2} are quadrate in occlusal view, with a posterolingual cusp (hypocone) separated from the protocone by a sulcus. M^3 does not develop a hypocone, but variants among even primitive taxa may show strong development of the cingulum in this region. The crest linking protocone to paracone (preprotocrista) is strong and is developed into a protoloph; on the first two molars, at least, and variably on M^3, a metaloph joins hypocone and metacone (Fig. 12). The metaconule of upper molars is expanded anterolabially into the trigon basin as a crochet; various other cuspules and crests characterize this part of most notoungulate upper molars (see Patterson, 1934; Simpson, 1948). Cingula are present anteriorly and posteriorly but not lingually. The posterior lower premolars (P_{3-4}) are molarized (P_3 somewhat less than P_4): the trigonid is crescentic, with crests directed anteriorly and posterolingually from the protoconid; the talonid is much shorter than the trigonid and also bears a crescentic crest. The construction of the lower molar trigonids is extraordinary, and the homol-

ogies of some parts are open to question. A crest (paracristid?), variable in length, extends anteriorly or anterolingually from the protoconid; a low anterior crest or cingulum, on the anterior face of the tooth, may connect with this in heavy wear so that the paracristid (?) appears to run to the lingual margin of the tooth. The greatest variation occurs in the region of the metaconid. That cusp may be anteroposteriorly expanded (Henricosborniidae, some Oldfieldthomasiidae), bearing an anterolabial-posterolingually directed crest. Another variant involves the presence of an anterior accessory cusp, which sometimes bears the appearance of a paraconid that has lost the paracristid connecting it to the protoconid (most notably in Isotemnidae but also in some Oldfieldthomasiidae). Notostylopids are characterized by an accessory cusp on the crest linking protoconid to metaconid (protocristid), so that this crest is serially tricuspid. Marshall, de Muizon, and Sigé (1983) propose homologies for these trigonid structures, which they argue are variations about a basic notoungulate pattern that included a pre- and postmetastylid. The talonid consists, in its simplest form (Henricosborniidae), of a crescent (cristid obliqua and postcristid) uniting hypoconid and hypoconulid, which nonetheless are retained as distinct, cusp-like entities. The entoconid is developed transversely (entolophid) and, in advanced forms, joins the postcristid anterior to the hypoconulid. The most primitive condition of this feature is seen in henricosborniids such as *Henricosbornia* itself. The entolophid is incompletely developed, posterobucally oriented, and is somewhat more separated from the hypoconulid on the posteriormost molar of Henricosborniidae. On M_1, however, this crest runs labially to the hypoconulid or to a point just anterior to that cusp, and it therefore appears that the entolophid is homologous to the crest connecting entoconid and hypoconulid (a portion of the postcristid), and becomes distinct as a separate loph by migrating anteriorly.

DISCUSSION

In the original description of the species, Matthew (1915) referred *Arctostylops steini* to the order "Entelonychia" and, within that group, placed the species with some doubt in the Isotemnidae. At that time, "notoungulate" to many students (see, e.g., the influential classifications of Gregory, 1910; Osborn, 1910; and Scott, 1904) was equivalent to "indigenous South American ungulate," and did not explicitly refer to that group in the sense it is defined today[8]. "Entelonychia" was a suborder proposed by Ameghino (1894) to include the aberrant, clawed *Homalodotherium* (a Santacrucian, mid-Miocene form shown by Patterson, 1936, to be toxodont-like in the construction of its ear region and since universally placed in the Toxodonta, a suborder of the Notoungulata) within the "Ancylopoda," thus uniting it with the similarly clawed chalicotheres of Holarctic faunas. Ameghino had abandoned the use of the term "Entelonychia" by the time of his final (1906) classification, but by this time had placed other notoungulate families (Isotemnidae and Leontiniidae, both currently recognized as belonging to the Toxodonta) with the Homalodotheriidae in the "Ancylopoda." The dentition of members of all these families are relatively primitive within the Notoungulata. Thus, later workers ignored Ameghino's reference of these and other notoungulates to Holarctic groups, and instead resurrected his term "Entelonychia" to include generally primitive notoungulates. (Scott, 1913, for instance, placed the Notostylopidae under this heading.) At the time of Matthew's (1915) writing, "Entelonychia" referred to primitive notoungulate mammals; then, as now, the Isotemnidae were considered to be basal members of the South American notoungulate radiations (although the henricosborniids are generally acknowledged to be somewhat more primitive).

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[8] The concept of the Notoungulata now current had, however, been made clear by Roth, 1903

Matthew and Granger (1925) recognized that *Palaeostylops iturus* was strongly specialized in having high-crowned cheek-teeth with well-developed shearing surfaces, and in having reduced lower molar trigonids. In this respect, they indicated that (pp. 4–5), "it may be regarded as ancestral to *Arctostylops* and through that genus to some of the South American Eocene Notoungulata (e.g., *Leontinia*, *Notostylops*, etc.) but to the latter only in a broad way, as no one of the genera of the Deseado fauna can be cited as clearly following the line indicated by *Palaeostylops-Arctostylops*." Nonetheless, as implied in the foregoing statement, they regarded *Palaeostylops* as more primitive in a number of features (for instance, the simple premolars) than the earliest of the South American notoungulates or *Arctostylops*. They thus believed the Asian genus to be ancestral, at least in a general sense, to all New World forms, and that "the South American Tertiary hoofed mammals were originally derived from the north, although undergoing a great secondary evolution in the Neotropical region" (p. 2).

Simpson (1934) clearly defined the Notoungulata and its contents. He removed the Arctostylopidae and Notostylopidae (a group of primitive South American notoungulates) from the "Entelonychia" and placed them with the Henricosborniidae in a then new paraphyletic suborder, Notioprogonia, defined on the basis of primitiveness of its constituent taxa. This left the "Entelonychia" as Ameghino had originally conceived it except that Simpson removed the Leontiniidae to the Toxodonta. Thus recognized, the Notoungulata comprised four suborders: Notioprogonia, "Entelonychia," Toxodonta, and Typotheria. On the basis of further studies (Patterson, 1936; Simpson, 1936b), Simpson later (1945) removed the remaining contents of the "Entelonychia" (Isotemnidae and Homalodotheriidae) to the Toxodonta, where they have since remained.

Simpson's view, elaborated in his two memoirs devoted to the earliest South American mammal faunas (Simpson, 1948, 1967), was that the Henricosborniidae, then known only from the Riochican and early Casamayoran (Cifelli, 1985b), or putative late Paleocene and early Eocene (Marshall, 1985; Marshall, Hoffstetter, and Pascual, 1983), represent the most primitive of known Notoungulata. By this interpretation, the order arose in South America from the same "ungulate" stock which gave rise also to the other groups of indigenous South American ungulates. Migration of a primitive notoungulate to North America and thence to Asia would thus provide the source for the Arctostylopidae (Simpson, 1951, 1965, 1978, 1980). Szalay and McKenna (1971) followed Simpson in this respect, noting that molars of then known arctostylopids were more advanced than any in the earliest South American notoungulates. Apparent support for a southern origin of the Notoungulata, on both morphological and temporal grounds, is lent by the proposed referral of *Perutherium*, from the Late Cretaceous of Peru, to the order (Marshall, de Muizon, and Sigé, 1983). Placement of this genus, which is based largely on two broken molars of the type and only species, has been a matter of considerable dispute since its initial description (Grambast *et al.*, 1967), with workers variously suggesting arctocyonid (Grambast *et al.*, 1967), didolodontid (Tedford, 1974), periptychid (Van Valen, 1978), and even marsupial (Hoffstetter, 1981) affinities. Marshall, de Muizon, and Sigé (1983) suggested that *Perutherium* possesses, in common with notoungulates, a pre- and postmetastylid in the trigonid of the lower molars, and that the genus is a morphologically appropriate antecedent to both the South American notoungulates and the Arctostylopidae.

Patterson (1958; Patterson and Pascual, 1972), on the other hand, followed Matthew (1928; Matthew and Granger, 1925) in believing that notoungulates arose in the north and, along with several mammalian companions, colonized South America in the earliest Tertiary, later to radiate and flourish on that continent. The basis for this opinion is unclear, but it is likely that

Patterson, like Matthew before him, was impressed by the early records of Arctostylopidae in North America (then thought to be early Eocene) and Asia (latest Paleocene), and by several of the strikingly primitive dental features found in members of that family. An Asian origin for the Notoungulata was also suggested by Nesov (1987). Gingerich and Rose (1977) proposed yet another possibility, that the Notoungulata arose in Central America (where evidence bearing on this issue is lacking) and from there spread both northward and southward.

Because of the inferred primitiveness of *Asiostylops* within the Notoungulata (simple premolars, triangular upper molars lacking a hypocone, simple molar lophs, unreduced anterior wing of lower molar trigonids), Zheng (1979) suggested that the order originated in Asia and, more specifically, in southern China. Earliest records need not infallibly indicate centers of origin, however. Van Valen (1988) considered *Asiostylops* to be sufficiently primitive to be structurally antecedent to trigonostylopids (an archaic group of Astrapotheria, which are endemic to South America).

Several recent studies have emphasized the profound differences in dental specializations between the Notoungulata and the Arctostylopidae, and on this basis have tentatively disassociated Holarctic from South American forms (Cifelli, 1983a, 1985a; Schaff, 1985; Thenius, 1985). It is well worth pointing out that it was Simpson who first flirted with this possibility, before returning to a more traditional view in the same paper:

> "A possibility that seems not to have been considered but perhaps should be is that *Arctostylops*, *Palaeostylops*, and *Sinostylops*, although quite surely related among themselves, might not after all be true notoungulates. Their dentitions do have derived characters that occur in almost all early notoungulates with various modifications and some marked changes in later, more specialized forms. These apparently diagnostic characters are not known in any other defined order of mammals. Nevertheless, these are unlike South American notoungulates in detail and one cannot absolutely exclude the possibility of convergence." (Simpson, 1978, p. 325)

Possible Relationships

Evaluation of these contrasting views on the origin and subsequent dispersal of the Notoungulata, of great interest in both zoogeographical and paleobiological terms, is dependent on determination of morphocline polarity sequences and the robustness of the phylogenetic framework derived therefrom. The issue of fundamental interest, one which remains to be examined in detail, is the phylogenetic position of the Arctostylopidae with respect to South American Notoungulata. Assuming notoungulate monophyly, inclusive of the Arctostylopidae, three possibilities present themselves: 1) arctostylopids took origin from a southern notoungulate as that group is known (southern origin); 2) the southern notoungulates derived from a form that falls within the Arctostylopidae as that group is here conceived (northern origin for the order); and 3) the Arctostylopidae and known South American Notoungulata are sister taxa (northern or southern origin).

Even without knowledge of the cranial morphology of arctostylopids (a suite of synapomorphies characterizes this region in notoungulates; Simpson, 1948), there is rather imposing evidence, in the dentition and proximal ankle, that the southern Notoungulata constitute a monophyletic assemblage. Derivation of the Arctostylopidae from within the order as it is currently recognized would require many simplifications (reversals) in the dentition, because *Asiostylops* in many cases and all arctostylopids in some instances are more primitive than any known southern notoungulate. The most significant of these

characters are in the upper molars. All southern notoungulates have secondary complications, consisting of at least a crochet (Patterson, 1934; Simpson, 1948) in the trigon basin on all upper molars and a hypocone on M^{1-2}; all arctostylopids lack the first character and at least *Asiostylops* among that family lacks either a hypocone or hypocone-like structure. By analogy with a series of variants in M^3 of *Henricosbornia lophodonta* (Fig. 12), which are not quadritubercular but which illustrate a plausible character state series for the addition of the posterolingual cusp on primitive notoungulate anterior upper molars, the posterointernal cusp of southern notoungulates appears to be a derivative of the cingulum and therefore a "true" hypocone (Simpson, 1929). By contrast, in arctostylopids which have quadritubercular M^{1-2}, the posterointernal cusp is encircled basally by the cingulum and appears to have originated as a transverse, lingual extension of the metacrista from the region of the metaconule[9]. Thus, the posterolingual upper molar cusp of southern notoungulates and arctostylopids appears to have been acquired independently and in a nonhomologous fashion.

Even the most primitive of southern Notoungulata (Henricosborniidae) have submolariform posterior lower premolars; P_4 has a complete, curved talonid crescent. Although the serially multicuspate, blade-like lower premolars of such forms as *Palaeostylops* may reflect specialization for shearing (secondary simplification), *Asiostylops* lacks the degree of molarization seen even in henricosborniids.

The proposed addition of *Perutherium altiplanense* to the Notoungulata (Marshall, de Muizon, and Sigé 1983) presents further problems for an origin of the Arctostylopidae within that group. Marshall, de Muizon, and Sigé (1983) suggest that the various accessory trigonid structures of notoungulates may be homologized with a pre- and a postmetastylid and that these are primitive for the order. Unlike typical South American notoungulates and the Arctostylopidae, *Perutherium* lacks an entolophid on its lower molars. The absence of a pre- and postmetastylid in *Asiostylops* and *Bothriostylops* would therefore require postulation of secondary loss of these structures in forms which otherwise seem to be rather primitive in the construction of their lower molars. Thenius (1985) accepted the lower molar pre- and postmetastylid pattern as a synapomorphy of notoungulates, and excluded arctostylopids from the order because it was lacking from "*Palaeostylops steini.*"

The morphotype for the notoungulate proximal ankle bones is not strongly specialized (as compared, for instance, to ungulate groups such as the Litopterna, Perissodactyla, Artiodactyla, and Hyracoidea, all of which are highly modified at first appearance in the fossil record). Nonetheless, it is characterized by a number of synapomorphies which render it readily recognized (Cifelli, 1983b). These features include a long, constricted astragalar neck, with an oblique dorsal crest; astragalar body with a median (tibial) protuberance; astragalar foramen with posterolateral sulcus interrupting continuity of tibial trochlea and flexor tendon groove; and well-developed sustentacular-navicular facet contact on the astragalus.

Except for a constricted astragalar neck, none of these features is shared with known arctostylopid ankle regions (*Gashatostylops macrodon* and *Palaeostylops iturus*), which bear specializations contrasting with those of notoungulates. The arctostylopid ankle is advanced in having an astragalus with a cylindrical, vertically-walled body, the tibial trochlea extensively developed anteroposteriorly; lack of a fibular shelf; navicular facet developed so that the axis of movement along the midtarsal joint would have been roughly parallel (rather

[9] Cifelli (1983a, p. 40) considered the posterointernal cusp of arctostylopid upper molars to be a displaced and transversely expanded metaconule; it appears, however, that the upper molar conules were [illegible] arctostylopid evolution.

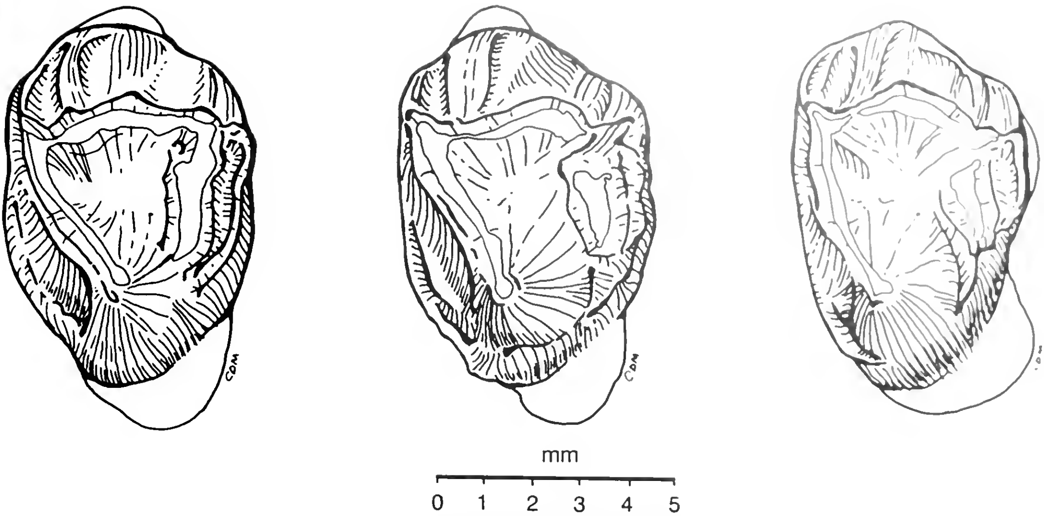


Figure 12. M³ variants in *Henricosbornia lophodonta*, AMNH 28964, from the early Casamayoran Cañadon Vaca local fauna, illustrating hypothesized addition of hypocone through linking of postcingular cusp and metaloph.

than oblique) to that at the proximal ankle joint; astragalar cuboid facet lost (?); ectal facet steeply inclined with respect to inferior surface of astragalus; calcaneal fibular facet strongly developed into a semicylindrical surface; and sustentaculum of calcaneus distally located, at or near distal (cuboid) end of the bone. Most of these ankle modifications are usually associated with restriction of lateral and inversion/eversion movement, with concomitant greater capability for flexion/extension, at the proximal and mid-tarsal joints. Such specializations are commonly found among terrestrial mammals (Cifelli, 1983b). The extreme distal position of the astragalocalcaneal facets on the calcaneus (a primitive condition?), implying poor mechanical advantage for rapid flexion of the pes by the gastrocnemius and soleus muscles, is enigmatic in this regard, and contrasts with the condition seen in terrestrial saltators or cursors. In any event, regardless of the paleobiological implications of this unusual ankle morphology, it is clear that notoungulates are uniquely derived with respect to arctostylopids, and vice versa.

Derivation of southern notoungulates from the Arctostylopidae (Matthew and Granger, 1925; Patterson, 1958; Zheng, 1979) is also contradicted by the available morphological evidence. Neotropical Notoungulata have a different style of upper premolar molarization from that of arctostylopids and lack a metacone on P³⁻⁴. The lower molars of henricosborniids show a very primitive state in the development of the typical notoungulate talonid: the major cusps (entoconid, hypoconid, hypoconulid) remain distinct; the entolophid is weak. The placement and orientation of the entolophid suggest that it was derived from the entoconid to hypoconulid part of the postcristid. Even in primitive arctostylopids (e.g., *Asiostylops*), the hypoconid is indistinct, having been merged into the talonid crescent. The entolophid of arctostylopids is advanced in being more anteriorly placed and is oriented anterolabially (Schaff, 1985). If *Perutherium* is a notoungulate, as argued by Marshall, de Muizon, and Sigé (1983), then derivation of South American taxa from arctostylopids would require independent acquisition of the entolophid in the Neotropical forms, because that structure is lacking in *Perutherium*.

The final possibility is that known Arc-

tostylopidae and southern Notoungulata are sister taxa: that they shared an ancestor that was exclusive to them and no other group of mammals. This hypothesis would be compatible with all existing scenarios regarding the geographic origin and dispersal of notoungulates. With the addition to the Arctostylopidae of primitive forms such as *Asiostylops* and *Bothriostylops*, nearly all of the similarities shared by southern notoungulates and advanced arctostylopids would have been acquired independently and therefore represent parallelisms. These include the reduction of the lower molar trigonids, the addition of accessory trigonid structures to those teeth (the homology of these structures, termed pre- and postmetastylid by Marshall, de Muizon, and Sigé, 1983, is open to some question, even among the taxa restricted to South America), the development of a talonid on P_4, and the upper molar crown pattern, which is superficially similar but appears on other grounds to include non-homologous features, as discussed above. What is known of the ankle region in arctostylopids indicates that they are divergently specialized from notoungulates. One specialization of the arctostylopid ankle, the development of the calcaneal fibular facet into a large, semicylindrical surface, is found among a group of advanced toxodont Notoungulata (the monophyletic group including Notohippidae, Leontiniidae, and Toxodontidae), but this was clearly developed independently by them. Certain other notoungulate resemblances of arctostylopids, which undoubtedly influenced early workers in their comparisons and in their speculation regarding relationships, evidently represent derived character states within *both* groups and are almost certainly convergent. These include the presence of a labial ectocingulid, which is characteristic of most toxodont lower molars and premolars and of advanced forms (e.g., *Palaeostylops*, *Gashatostylops*, and *Arctostylops*) among the Arctostylopidae. The smooth ectoloph of advanced arctostylopid upper molars (*Anatolostylops*; unnamed genus and species), which lacks folds other than those for the parastyle and metastyle, is reminiscent of that of notoungulates such as *Notostylops* (comparison with which was the basis for the genus and family-group names of the northern forms) and various Leontiniidae, but primitive members of both the Arctostylopidae and southern Notoungulata have lower, more complexly folded ectolophs. *Arctostylops* and ?*Palaeostylops* also resemble some southern notoungulates, especially *Notostylops*, in the high talonid crescent, which achieves an anterior attachment with the trigonid at a very labial position; this, again, is not a condition shared by more primitive members of either group.

Remaining Resemblances

With the dismissal of many arctostylopid-notoungulate similarities as convergent acquisitions within each group, it is relevant to evaluate the uniqueness of resemblances that remain. The most striking of these is the transversely developed, lophate entoconid (entolophid) of the lower molars. This is an unusual but not exceptional feature among mammals: it surely developed independently in the Astrapotheria and twice among the Litopterna (Cifelli, 1983a; Cifelli and Soria, 1983). Among Holarctic mammals, an entolophid or similar structure developed independently in numerous rodent lineages (L. L. Jacobs, personal communication). Without knowledge of more primitive forms, it is not possible to determine if the arctostylopid entolophid arose, as in the southern notoungulates, from part of the postcristid or if it is demonstrably non-homologous (the entolophid of astrapotheres, for instances, appears to be a *de novo* structure). If, as argued by Marshall, de Muizon, and Sigé (1983), *Perutherium* is a notoungulate, then independent acquisition of the entolophid in the Arctostylopidae is suggested by the fact that they primitively lack the accessory trigonid structures possibly shared by that genus with Neotrop-

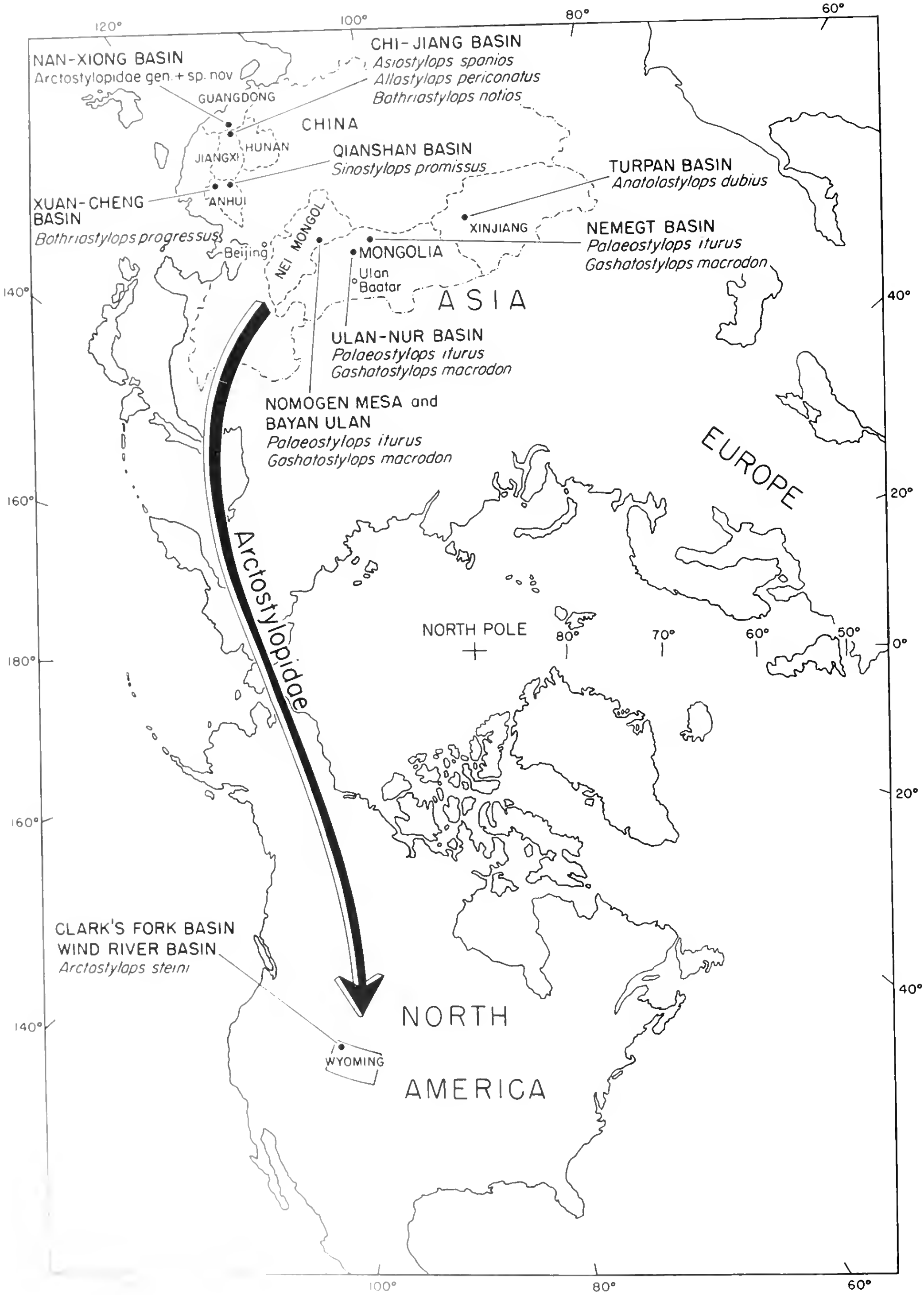
ical Notoungulata. Other shared dental features of arctostylopids and notoungulates, derived with respect to an ungulate morphotype, might include a crescentic lower molar trigonid (this condition is somewhat uncertain in southern notoungulates, as the trigonid is already reduced at first appearance), reduced upper molar stylar shelf and lobes, and slightly raised centrocrista between paracone and metacone on the upper molars ("incipient" ectoloph). These latter features are not in themselves or collectively diagnostic, as they represent generalized, almost gradal trends in many different groups of Paleocene and Eocene ungulate-like mammals.

Of the three alternatives of arctostylopid-notoungulate relationships discussed above, the most permissive, that they represent sister taxa, is the most likely. (This is true by definition, as the other two possibilities are more specific and therefore more susceptible to falsification.) Yet, because most similarities of arctostylopids to notoungulates must have arisen independently, whether by parallelism or convergence, the evidence that they collectively comprise a monophyletic unit with respect to other mammals is slim: it amounts, in fact, to one possible character (entolophid) that is known to have developed independently several times among other, unrelated groups. This is hardly secure documentation of monophyly. Other evidence, such as that provided by the ankle region, suggests that a common ancestor of the two groups would have been exceedingly primitive and, probably, not exclusive.

Distinctness of Arctostylopida

Since the time of Ameghino, many close relationships of South American with Holarctic forms have been proposed (see, e.g., summaries by Simpson, 1978; McKenna, 1981; and Gingerich, 1985). With the exception of marsupials, the controversy surrounding all ordinal and lower level referrals of South American to Holarctic taxa has been considerable, in part because derived similarities are incomplete or not unambiguously homologous, and in part because the evidence of relationship has often been based on shared primitive features rather than uniquely derived specializations. The Arctostylopidae have been immune to such controversy because, despite some unique aberrancies and retention of a few primitive features, the advanced genera *Arctostylops* and *Palaeostylops* strikingly resemble notoungulates and no other mammals in certain aspects of their dental anatomy. Evaluation of the reality of this relationship and its precise nature was long hampered by insufficient knowledge of arctostylopid morphologic diversity and of the structure and relationships of the most primitive notoungulates of South America. With these circumstances now dramatically improved, considerable doubt is cast on the close relationship of the two groups, accepted without question for most of this century. A common notoungulate/arctostylopid ancestor (i.e., a morphotype for the two groups, considered as sister taxa) might have been sufficiently primitive to have given rise to many other orders of mammals. In recognition of this, and considering the ample evidence for monophyly of the Arctostylopidae, we have referred the family to its own order. Thus recognized, the group would represent an Asian radiation that managed to disperse to North America, possibly in the late Paleocene. The geographic distribution of arctostylopid taxa, and the hypothesized immigration to North America, are given in Figure 13. It is interesting to note that most of the primitive forms are more southerly in distribution, being found in south China, while specialized taxa are generally northerly in distribution.

The broader relationships of Arctostylopida among the Mammalia are enigmatic. The arctostylopid dental morphotype bears some similarity to several Asian taxa of debatable affinities, such as *Lantianius* (Cifelli, 1983a) and *Petrolemur*, although contrasting specializations (such as loss of premolars in the latter genus) are


NAN-XIONG BASIN
Arctostylopidae gen. + sp. nov
GUANGDONG
CHI-JIANG BASIN
Asiostylops spanios
Allostylops periconatus
Bothriastylops notios
CHINA
HUNAN
JIANGXI
QIANSHAN BASIN
Sinostylops promissus
TURPAN BASIN
Anatolostylops dubius
XUAN-CHENG BASIN
Bothriostylops progressus
ANHUI
XINJIANG
NEMEGT BASIN
Palaeostylops iturus
Gashatostylops macrodon
Beijing
NEI MONGOL
MONGOLIA
Ulan Baatar
ASIA
ULAN-NUR BASIN
Palaeostylops iturus
Gashatostylops macrodon
NOMOGEN MESA and
BAYAN ULAN
Palaeostylops iturus
Gashatostylops macrodon
EUROPE
Arctostylopidae
NORTH POLE
CLARK'S FORK BASIN
WIND RIVER BASIN
Arctostylops steini
WYOMING
NORTH
AMERICA
120°
100°
80°
60°
140°
160°
180°
40°
20°
0°
70°
50°

evident. Both forms were originally referred to the Primates; the ankle of known arctostylopids is completely dissimilar to any belonging to that order. Arctostylopid ankle specializations are shared, as best we are able to determine from published figures (Sulimski, 1968; Szalay, 1977, fig. 16), with the Asian late Paleocene *Pseudictops*. This taxon has, in turn, been considered to be part of "an endemic Cretaceous and early Tertiary Asian radiation, whose closest living relatives are the Lagomorpha" (Szalay and McKenna, 1971, p. 301). Whatever the constituents of this radiation (see also McKenna, 1975; Novacek, 1986; Szalay, 1977), we note that lagomorphs and some of their suspected allies are specialized for saltatory locomotion (Szalay, 1977; see Bleefeld and McKenna, 1985, for description of some lagomorph ankle specializations); arctostylopids—which may just be primitive in this regard—apparently were not, as indicated by the lever mechanics of the calcaneus.

The diversity and abundance of arctostylopids in early Tertiary Asian faunas, coupled with the proposed close relationship of North American *Arctostylops* to Asian *Palaeostylops* as rather derived taxa within the family, suggests that dispersal from west to east, rather than the reverse, is the most probable explanation for geographic distribution of the group. Owing to high endemism of Asian faunas older than those of the North American Wasatchian, correlation of earliest Tertiary mammalian assemblages between the two continents has been problematic (Szalay and McKenna, 1971). The presence of *Arctostylops* in the Tiffanian (late Paleocene) of North America, the geometry of proposed relationships among the Arctostylopidae, and the fact that more primitive taxa are known from Asia but not North America, suggest a late Paleocene (Dashzeveg, 1982; Szalay and McKenna, 1971), rather than early Eocene (Gingerich and Rose, 1977) age for Asian faunas, such as Gashato, which include *Palaeostylops* and *Gashatostylops*.

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Figure 13. Lambert's azimuthal equal area projection map of Northern Hemisphere, showing arctostylopid distribution and hypothesized dispersal route to North America.

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PRIMARY TYPES OF MICROLEPIDOPTERA IN THE MUSEUM OF COMPARATIVE ZOOLOGY (WITH A DISCURSION ON V. T. CHAMBERS' WORK)

SCOTT E. MILLER[1] and RONALD W. HODGES[2]

ABSTRACT: Primary types (holotypes, lectotypes and syntypes) in the moth superfamilies Eriocranioidea, Hepialoidea, Nepticuloidea, Incurvarioidea, Tineoidea (except Gracillariidae), Gelechioidea (except Coleophoridae), Copromorphoidea, Yponomeutoidea, Sesioidea, Cossoidea, Tortricoidea, Zygaenoidea, Pyraloidea, and Pterophoroidea are listed.Most of the taxa are Nearctic, several Neotropical. Authors included are S. E. Cassino, V. T. Chambers, W. G. Dietz, H. Edwards, C. Fish, W. T. M. Forbes, H. Frey and J. Boll, A. R. Grote, T. W. Harris, G. D. Hulst, W. D. Kearfott, A. S. Packard, Lord Walsingham, and P. C. Zeller. Lectotypes are designated herein for *Anacampsis quadrimaculella* (Chambers) and *Isophrictis trimaculella* (Chambers) (both Gelechiidae).

INTRODUCTION

Classification of several groups of North American microlepidoptera is made very difficult because most early workers on this fauna did not designate type specimens; their descriptions are inadequate to recognize the species; their "type" material was sent to more than one institution; and among them they described several hundred species. The Museum of Comparative Zoology (MCZ), Harvard University, has a significant number of types of these authors, particularly of V. T. Chambers. Chambers is notorious for his very brief and inadequate descriptions, the large number of his often very short papers in scattered journals, the large number of species for which no type material exists, and for the fact that his types were dispersed among the MCZ and contemporary workers. Because we have studied Chambers' papers and believe we have uncovered nearly all remaining specimens that can be considered authentic, we have included a discussion of specimens in other collections (see Appendix) and Chambers' bibliography to apprise other workers of the facts they will need when selecting lectotypes or designating neotypes. Many species are represented by no extant type material or are not represented by specimens in the MCZ; their names do not appear in the catalog.

This catalog lists the primary types of 609 taxa of Microlepidoptera located in the MCZ. All holotypes, lectotypes, and syntypes in the families treated are listed along with some paralectotypes and "pseudotypes." All specimens (except obvious paratypes) with numbered red "M.C.Z. type" labels are included. These red numbered labels were placed on the specimens by Nathan Banks and subsequent curators and sometimes are not accurate as noted in this list. Some lectotypes have been designated by previous authors by inference of holotype (Article 74(b), International Code of Zoological Nomenclature, third edition, 1985). For example, a lectotype was designated for *Nepticula castaneaefoliella* Chambers by inference of holotype. We have not designated additional lectotypes here (except for two as part of

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Hodges' research) because this action should be left to specialists as part of the revision process. Each species-group entry has five potential topics: 1) Original combination, author, and date-page citation; 2) Category of type, sex of specimen(s), and MCZ type number; 3) Geographic distribution as indicated in the original description and/or labels accompanying the type specimens; 4) Current valid name (if different from original combination); and 5) Remarks.

Information presented in brackets [ ] represents additions to or corrections of the original description. The present valid name of each taxon listed, if it differs from the original combination, is also included (following Hodges, et al., 1983 and more recent literature). Sex is included only when it could be determined readily without damaging the specimen. The locations of some other syntypes are indicated if known, using the following abbreviations: AMNH = American Museum of Natural History, New York; ANSP = Academy of Natural Sciences, Philadelphia; BMNH = British Museum (Natural History), London; LACM = Natural History Museum of Los Angeles County, Los Angeles; and USNM = National Museum of Natural History, Smithsonian Institution, Washington.

The following superfamilies (following Hodges, et al., 1983) are included in the list: Eriocranioidea, Hepialoidea, Nepticuloidea, Incurvarioidea, Tineoidea (except Gracillariidae), Gelechioidea (except Coleophoridae), Copromorphoidea, Yponomeutoidea, Sesioidea, Cossoidea, Tortricoidea, Zygaenoidea, Pyraloidea, and Pterophoroidea. Data for Tineidae and Blastobasidae were provided by D. R. Davis and D. Adamski, respectively. Gracillariidae are under study by D. R. Davis (USNM). Coleophoridae are under study by B. Wright (Nova Scotia Museum) and were discussed by McDunnough (1944).

All the types listed here are in the main MCZ collection, except those in the Harris collection, which is maintained separately from the general collection. The MCZ collection includes the Peabody Academy collection (the Peabody Academy still exists in Salem, Massachusetts, but no longer maintains entomological collections) and the types from the now defunct Boston Society of Natural History. Details on the major type collections discussed here follow:

Vactor T. Chambers: Most of the remains of the Chambers collection are at the MCZ, with another significant part at the USNM. See appendix for discussion of possible Chambers types at the BMNH. Chambers deposited types at the MCZ between 1876 and 1883 (Hagen, 1884); many of them are in very poor condition, and many probably are not true types but specimens substituted by Chambers for lost or damaged types.

Walsingham (1889: 24) wrote, "Chambers, in distributing specimens to his various correspondents, frequently appears to have attached a wrong name to them. This he admits in more than one instance in his writings. The utmost caution is required before accepting a specimen in any collection as a co-type of any one of his species."

Chambers (1877c: 39) wrote: ". . . But a few years ago I began to make a collection to be preserved as types of all my species. These were all pinned and spread. Unfortunately, during my absence in Colorado, the greater part of this collection was destroyed. One or more specimens of the greater number of species were fortunately preserved, and most other species can be supplied. This collection is now in the Cambridge Museum [MCZ]. It contains types — pinned and spread — of something over 200 species." (See also Braun, 1963: 2; Hagen, 1884; Sattler, 1962.)

Most Chambers specimens bear only the data "Kentucky./Chambers." (machine printed) along with a handwritten determination label, and frequently a large handwritten number (between 12 and 164) on a separate label (the meaning of which remains unknown). Most of these were presumably collected around his home in

Covington, Kentucky (Chambers, 1875b: 234). Chambers wrote (1872: 433), "Out of at least one hundred and fifty species of Tineina which I have found here, fully three-fourths have been taken resting upon the leeward side of a board fence not two hundred yards long, at Linden Grove Cemetary at this place [Covington, Kentucky]."

Other major lots of material include those collected by Chambers (and others) in Colorado in 1875 (and other years) and Texas specimens purchased by Chambers from Gustaf W. Belfrage. Belfrage lived near Norse, Bosque County (some 60 km northwest of Waco), Texas, from 1868 to 1882 (Geiser, 1948). Most, but not all, of Belfrage's moth material was probably collected there.

The USNM has many Chambers types, obtained primarily through acquiring the collections of C. H. Fernald (which included part of the M. Murtfeldt collection), F. H. Belanger (via Laval University, Quebec), and W. Saunders (Busck, 1903: 768).

Type localities for many of Chambers' species are not obvious from the original descriptions. We have followed the label data on the types, unless contradicted by other evidence.

Because of the scattered nature of Chambers' publications, we have included all of them on Lepidoptera in our literature section, whether mentioned here or not.

William G. Dietz: His types of Blastobasidae and Gracillariidae are in the MCZ.

Heinrich Frey and Jacob Boll: Several types of species described by Frey and Boll (1873) previously assumed to be at the BMNH (e.g., Braun, 1972: 56) are present. These were evidently collected by Boll around Cambridge, Massachusetts, in autumn 1871 (Geiser, 1948: 22–23).

Thaddeus W. Harris: Probably the oldest extant collection of North American insects, most specimens are still in good condition. It is held as a separate unit at the MCZ because the labels are cryptic (Johnson, 1925). Most specimens bear Harris numbers, the catalog of which is in the MCZ Archives. Specimens for which further data are not given probably came from Massachusetts.

George D. Hulst: As discussed by Rindge (1955), the main Hulst collection is at AMNH, but the MCZ has syntypes of some Hulst taxa.

William D. Kearfott: The MCZ has a number of Kearfott syntypes (labeled "cotype"), some of which have now become paralectotypes. As discussed by Klots (1942: 392–393), much of Kearfott's collection is in AMNH, but parts are in USNM (via the Barnes collection), and elsewhere (including MCZ). The best candidates for lectotype designation for Kearfott taxa will generally be found at AMNH or USNM, not at MCZ. Authorship of lectotype designations in some Kearfott Tortricidae remains problematic; Klots (1942) credited many lectotype designations to Heinrich (1923, 1926). However, Heinrich did not publish which specimen he considered the type if there was more than one syntype in AMNH. Klots usually did designate individual specimens, and should be considered the designator of most of the lectotypes in question.

Alpheus S. Packard, Jr.: Included here are California specimens collected by Henry Edwards. Some of these Edwards specimens bear Edwards' catalog numbers; data from Edwards' catalog (now in AMNH) are included here.

Lord Walsingham [Thomas de Grey]: The MCZ has one Walsingham holotype (Eriocraniidae) and many syntypes (Oecophoridae and Plutellidae). The syntypes are duplicates of species described by Walsingham (1881) from material he collected in California and Oregon in 1871–72 (see Essig, 1941), which were sent to Chambers by Walsingham. Lectotypes for these taxa should be designated from syntypes in the Walsingham collection at the BMNH.

Philipp C. Zeller: The MCZ has most of the specimens collected by Jacob Boll around Dallas, Texas in late 1869 and 1870

(Geiser, 1929, 1948) and described by Zeller in three papers on North American Microlepidoptera (1872, 1873, 1875). The Boll specimens were purchased by Louis Agassiz for the MCZ and sent to Zeller for study. They all bear characteristic labels: machine printed "Dallas, Tex. Boll" and handwritten Zeller determination labels on green paper.

The following corrections and additions to recent literature are noted in the list: Several types not located by Wilkinson and coauthors are included (Nepticulidae). The syntypes of 11 Harris species reported lost by Duckworth and Eichlin (1978) are included (Sesiidae). The following were accidently omitted from Hodges, et al. (1983): "*Elachista*" *texanella* Chambers (Scythrididae), *Paralipsa fulminalis* (Zeller) (Pyralidae) and *Marasmarcha pumilio* (Zeller) (Pterophoridae). Problems are noted in previous lectotype selections for *Pyrausta unifascialis* (Packard) (Pyralidae) and *Oidaematophorus grandis* (Fish) (Pterophoridae). LECTOTYPES are here designated for *Anacampsis quadrimaculella* (Chambers) and *Isophrictis trimaculella* (Chambers) (both Gelechiidae). "*Scythris*" *albapenella* (Chambers) is here transferred from Scythrididae to Blastobasidae on advice of J. F. Landry and D. Adamski; Adamski will deal with its generic placement in a subsequent publication.

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SUPERFAMILY ERIOCRANIOIDEA

Family Eriocraniidae

auricyanea Walsingham, 1882: 204, **Micropteryx** [sic]; HOLOTYPE male, MCZ 1622; [United States: probably California (see Davis, 1978)]; *Dyseriocrania auricyanea* (Walsingham).

SUPERFAMILY HEPIALOIDEA

Family Hepialidae

argenteomaculatus Harris, 1841: 295, **Hepiolus** [sic]; SYNTYPE, MCZ 26378; United States: [Massachusetts, Cambridge, Harris no. 257]; *Sthenopis argenteomaculatus* (Harris); Often cited as 1842, the description was originally published in 1841, and reprinted in 1842 (page 295 of both works).

labradoriensis Packard, 1864c: 394, **Hepialus**; HOLOTYPE [?] male, MCZ 160; Canada: Labrador, Straits of Belle Isle, Caribou Island, Salmon Bay, 3 August 1860, A. S. Packard, Jr.; *Korscheltellus gracilis* (Grote) (see Wagner, 1988); Abdomen and wings glued in place.

SUPERFAMILY NEPTICULOIDEA

Family Nepticulidae

apicialbella Chambers, 1873: 127, **Nepticula**; PARALECTOTYPES (5), MCZ 1496; United States: Kentucky, June, Chambers; *Stigmella apicialbella* (Chambers); Lectotype (USNM type 523) and 3 paralectotypes in USNM designated by Newton and Wilkinson (1982: 367).

bosquella Chambers, 1878c: 106, **Nepticula**; SYNTYPES (2 males), MCZ 14958; United States: Texas, Bosque County; *Ectoedemia obrutella* (Zeller); A male syntype in USNM (type 524).

castaneaefoliella Chambers, 1875a: 117, **Nepticula**; LECTOTYPE female, MCZ 14956; United States: Kentucky, Chambers; *Stigmella castaneaefoliella* (Chambers); Wilkinson and Scoble (1979: 46), designated the lectotype (Code, Art. 74(b)).

ciliaefuscella Chambers, 1873: 128, **Nepticula**; SYNTYPE, MCZ 1301; United States: Kentucky, "at lamp," 23 August [year not stated], Chambers; *Stigmella fuscotibiella* (Clemens).

clemensella Chambers, 1873: 125, **Nepticula**; LEC-

TOTYPE female, MCZ 14955; United States: Kentucky, Chambers; *Ectoedemia clemensella* (Chambers); Lectotype and paralectotype in MCZ by Wilkinson and Scoble (1979: 86).

grandisella Chambers, 1880b: 193, **Nepticula**; HOLOTYPE male, MCZ 1302; United States: Texas; *Ectoedemia grandisella* (Chambers).

juglandifoliella Chambers, 1878c: 105, **Nepticula**; SYNTYPE, MCZ 1495; United States: Kentucky, Chambers; *Stigmella juglandifoliella* (Clemens); Chambers (1878c) used Clemens' (1861) name for "mine and adult,"the mine of which was described by Clemens. Despite acknowledgement of Clemens' previous use, Chambers called his name a new species.

latifasciella Chambers, 1878c: 106, **Nepticula**; HOLOTYPE female, MCZ 1497; United States: Kentucky, "on . . . chestnut-trees," August, Chambers; *Stigmella latifasciella* (Chambers).

maculosella Chambers, 1880b: 193, **Nepticula**; HOLOTYPE female, MCZ 1303; United States: Texas; *Stigmella nigriverticella* (Chambers); Newton and Wilkinson (1982: 425) commented on status of this name.

maximella Chambers, 1873: 126, **Nepticula**; SYNTYPES (2), MCZ 14951; United States: Kentucky, Chambers; *Ectoedemia platanella* (Clemens); Not mentioned by Wilkinson and Scoble (1979) or Wilkinson and Newton (1981).

pomivorella Packard, 1870: 237, **Micropteryx**; SYNTYPE, MCZ 1499; United States: Massachusetts, Salem, A. S. Packard, Jr; *Stigmella pomivorella* (Packard); There are two specimens, an adult ("Imm. 12.[18]71") and a cocoon ("Apple June 19"), probably from the same individual as stated by Busck (1901: 52).

quericastanella Chambers, 1873: 127, **Nepticula**; SYNTYPES (3), MCZ 1304; United States: Kentucky, Chambers; *Stigmella saginella* (Clemens).

quercipulchella Chambers, 1878c: 105, **Nepticula**; HOLOTYPE male, MCZ 14957; United States: Kentucky, Chambers; *Stigmella quericipulchella* (Chambers).

resplendensella Chambers, 1875a: 118, **Nepticula**; LECTOTYPE, MCZ 14954; United States: Kentucky, 23 May [year not stated], Chambers; *Stigmella resplendensella* (Chambers); Lectotype designated by Newton and Wilkinson (1982: 456) who incorrectly stated it was in ANSP.

serotinaeella Chambers, 1873: 126, **Nepticula**; SYNTYPE, MCZ 1498; United States: Kentucky, Chambers; *Stigmella prunifoliella* (Clemens); Head and forewings only.

thoracealbella Chambers, 1873: 127, **Nepticula**; LECTOTYPE male, MCZ 14952; United States: Kentucky, June, Chambers; *Microcalyptris thoracealbellus*(Chambers); Wilkinson (1979: 70) designated the lectotype (Code, Art. 74(b)).

unifasciella Chambers, 1875a: 119, **Nepticula**; LECTOTYPE female, MCZ 1305; United States: Kentucky, Chambers; *Stigmella unifasciella* (Chambers); Lectotype and paralectotype also in MCZ designated by Newton and Wilkinson (1982: 440).

Family Tischeriidae

aenea Frey and Boll, 1873: 222, **Tischeria**; SYNTYPES (5), MCZ 1349; United States: Massachusetts, "Cambr.B." [=Cambridge, Boll or Cambridge, Boston]; Braun (1972: 56) stated "Type, Texas (probably Dallas)[BM]," but type locality is not specified in original description, and introduction to the paper indicates most of the species were reared by Boll at Cambridge.

badiiella Chambers, 1875a: 109, **Tischeria**; SYNTYPES (8), MCZ 14941; United States: Kentucky, Chambers; Braun (1972: 21) stated "Type? Kentucky (MCZ?); Type [female] Kentucky(?), genitalia slide 9707 J.F.G.C. (USNM)." USNM specimen is type 516.

clemensella Chambers, 1878c: 99, **Tischeria**; SYNTYPE, MCZ 14940; United States: Texas; Braun (1972: 34–35) stated type locality is Kentucky as implied by Chambers (1875a: 110, 1878c: 99), but specimen is labelled "Tex."

concolor Zeller, 1875: 352, **Tischeria**; HOLOTYPE female, MCZ 1348; United States: Texas, Dallas, Boll; Braun (1972: 27) stated "Type [female], Texas (MCZ)."

fuscomarginella Chambers, 1875a: 110, **Tischeria**; LECTOTYPE male, MCZ 14938; United States: Kentucky, Chambers; Braun (1972: 35) designated the lectotype (Code, Art. 74(b)).

heliopsisella Chambers, 1875a: 113, **Tischeria**; SYNTYPES (2), MCZ 1503; United States: Kentucky, Chambers.

latipenella Chambers, 1878c: 97, **Tischeria**; HOLOTYPE male, MCZ 14942; United States: Texas; *Tischeria zelleriella* Clemens.

pulvella Chambers, 1878c: 99, **Tischeria**; LECTOTYPE, MCZ 1505; United States: Texas; Braun (1972: 97) designated the lectotype (Code, Art. 74(b)).

purinosella Chambers, 1875a: 110, **Tischeria**; LECTOTYPE, MCZ 14939; United States: Kentucky, Chambers; Braun (1972: 29) designated the lectotype (Code, Art. 74(b)).

quercivorella Chambers, 1875a: 109, **Tischeria**; SYNTYPES (5), MCZ 1506; United States: Kentucky, Chambers; *Tischeria citrinipennella* Cle-

mens. Braun (1972: 15) stated "Type [male], Kentucky (MCZ)," but no specimen was labelled lectotype.

roseticola Frey and Boll, 1873: 223, **Tischeria;** SYNTYPES (2), MCZ 1350; United States: Massachusetts, "Cambr.B.", See comments under *Tischeria aenea* regarding type locality.

tinctoriella Chambers, 1875a: 108, **Tischeria;** SYNTYPE, MCZ 150, United States: Kentucky, Chambers; *Tischeria quercitella* Clemens; Two additional specimens, labelled only "Kentucky./ Chambers." may be syntypes also.

SUPERFAMILY INCURVARIOIDEA

Family Incurvariidae

alba Zeller, 1873: 232, **Tegeticula;** LECTOTYPE male, MCZ 2922; United States: Texas, Dallas, Boll; *Tegeticula yuccasella* (Riley); Lectotype designated by Davis (1967: 51).

aureovireus Dietz, 1905: 39, **Incurvaria;** HOLOTYPE, MCZ 2874; United States: Pennsylvania, Hazleton, [23] June 1899, Dietz; *Phylloporia bistrigella* (Haworth).

bella Chambers, 1873: 73, **Adela;** SYNTYPE female, MCZ 1402; United States: Kentucky, May, Chambers; *Adela caeruleella* Walker.

chalybeis Zeller, 1873: 226, **Adela;** HOLOTYPE male, MCZ 32960; United States: Texas, Dallas, Boll; *Adela caeruleella* Walker.

dietziella Kearfott, 1908: 187, fig. 6, **Incurvaria?;** SYNTYPES (4), MCZ 14236; United States: New Jersey, Essex County, 30 May 1907, W. D. Kearfott; *Chalceopla dietziella* (Kearfott).

paradoxica Chambers, 1878e: 149, **Hyponomeuta** [sic]; LECTOTYPE male, MCZ 32959; United States: Colorado, "nine miles north of Colorado Springs and thence 5 miles east of the mountains"; *Prodoxus quinquepunctellus* (Chambers); Lectotype and four paralectotypes also in MCZ designated by Davis (1967: 76).

5-punctella Chambers, 1875d: 7, **Hyponomeuta** [sic]; LECTOTYPE female, MCZ 1413; United States: Texas, Bosque County, *Prodoxus quinquepunctellus* (Chambers). Lectotype designated by Davis (1967: 75).

rheumapterella Dietz, 1905: 37, pl. 1: fig. 4, **Incurvaria;** LECTOTYPE female, MCZ 2873; United States. Colorado, Durango; *Prodoxus coloradensis* Riley. Lectotype and paralectotype also in MCZ designated by Davis (1967: 83).

Family Heliozelidae

aesella Chambers, 1877a: 108, **Heliozela;** HOLOTYPE, MCZ 1512, United States: Kentucky, near Covington, 24 April, Chambers; Head and right front wing only.

ampelopsifoliella Chambers, 1874a: 168, **Antispila;** PSEUDOTYPES (3), MCZ 1367; United States: Kentucky, Chambers; Chambers (1874: 168) states "known only in the larval state," so these cannot be types. One of the three specimens is missing from its minuten.

gracilis Zeller, 1873: 314, **Heliozela;** HOLOTYPE male, MCZ 1351; United States: Texas, Dallas, Boll.

viticordifoliella Chambers, 1874a: 168, **Antispila;** SYNTYPES (2), MCZ 1368; United States: Kentucky, Chambers.

SUPERFAMILY TINEOIDEA

Family Tineidae
Donald R. Davis

apachella Dietz, 1905: 7, **Amydria;** SYNTYPE female, MCZ 2904; United States: Arizona, Catal[ina] Springs; The type series of apachella is mixed. This specimen (MCZ 2904) is *curvistrigella* Dietz. One female syntype (Williams, Arizona) of *apachella* is in USNM.

apicisignatella Dietz, 1905: 65, **Tinea;** SYNTYPES (2 of 3), MCZ 2862; United States: New Hampshire, Hampton and Pennsylvania, Hazleton; *Nemapogon variatella* (Clemens); Both MCZ syntypes lack abdomens and one lacks a forewing. An additional female syntype is in USNM.

approximatella Dietz, 1905: 27, **Scardia;** PARALECTOTYPES (8), MCZ 2889 and 1 PSEUDOTYPE, MCZ 2889; United States: New Jersey, Essex County (Kearfott); and Pennsylvania, Hazleton, and Mauch Chunk; *Scardiella approximatella* (Dietz); One Hazleton, Pennsylvania, "syntype" bears a label date of "6/28/06" and therefore may not be a true type. Lectotype male and paralectotype female in USNM, designated by Robinson (1986: 109).

argentinotella Chambers, 1876b: 104, **Semele;** SYNTYPE female, MCZ 1400; United States: Kentucky, June, Chambers; *Homosetia argentinotella* (Chambers); No other syntypes are known.

arizonella Dietz, 1905: 6, **Amydria;** SYNTYPE male, MCZ 2903; United States: Arizona, Huachuca; Abdomen missing. Another male syntype (Phoenix, Arizona) in USNM.

auricristatella Chambers, 1873a: 110, **Pitys;** SYNTYPE female, MCZ 1397; United States: Kentucky, Chambers; *Homosetia auricristatella* (Chambers); No other syntypes are known.

auristrigella Chambers, 1873a: 86, **Tinea;** SYNTYPE male, MCZ 14943; United States: Kentucky, July, Chambers; *Isocorypha mediostriatella* Clemens; In

poor condition and glued to a paper point. No other syntypes are known.

auropulvella Chambers, 1873a: 90, **Tinea;** SYNTYPES (1 male, 2 females), MCZ 1391; United States: Kentucky, July; *Nemapogon auropulvella* (Chambers); Two additional male syntypes in USNM.

aurosuffusella Chambers, 1873a: 87, **Tinea;** SYNTYPE female, MCZ 1394; United States: Kentucky, Chambers; *Hybroma servulella* Clemens; No other syntypes are known.

behrensella Chambers, 1875b: 249, **Tinea;** HOLOTYPE, presumed lost; United States: Californa, San Francisco, J. Behrens.

bimaculella Chambers, 1873a: 87, **Tinea;** SYNTYPES (3 males), MCZ 1388; United States: Kentucky, Chambers; *Tinea mandarinella* Dietz; Chambers' name is preoccupied by Thunberg, 1794.

bipunctella Dietz, 1905: 77, **Progona;** HOLOTYPE female, [no MCZ number]; United States: Florida, Hastings; *Mea bipunctella* (Dietz); Specimen mostly destroyed, only fragments of mesothorax adhering to pin.

brevipennella Dietz, 1905: 5, **Amydria;** SYNTYPES (3 males), MCZ 2901; United States: District of Columbia, Washington, A. Busck; Maryland, Plummer's [sic] Island, A. Busck; Additional syntypes in USNM (13) and BMNH (3).

busckiella Dietz, 1905: 12, **Paraplesia;** PSEUDOTYPE female, MCZ 2892; United States: Arizona, Catal[ina] Springs, [E. A. Schwarz]; *Hypoplesia busckiella* (Dietz); Dietz (1905) states that the only material examined by him was a single male (therefore the holotype) in the USNM. Consequently the MCZ "cotype" and a male "cotype" in LACM are not true types.

carbonella Dietz, 1905: 30, **Abacobia;** SYNTYPES (1 male, 4 females), MCZ 2871; United States: Pennsylvania, Hazeleton, W. G. Dietz; *Elatobia carbonella* (Dietz); Two additional syntypes (male and female) in USNM.

cariosella Dietz, 1905: 17, **Epilegis;** SYNTYPE male, MCZ 2898; United States: California, Kaweah; *Setomorpha rutella* Zeller; Dietz described this species from two males from Kaweah, California. A female "cotype" in MCZ and another female "cotype" in LACM, both of which bear no locality labels, are not types.

chrysocomella Dietz, 1905: 43, **Isocorypha;** HOLOTYPE, MCZ 2883; United States: Kansas, Onaga, [H. Kahl].

clemensella Chambers, 1873a: 174, **Xylesthia;** SYNTYPES (3 males, 3 females, 2 unknown), MCZ 1384; United States: Kentucky, [Chambers]; *Xylesthia pruniramiella* Clemens; Four MCZ syntypes are badly damaged with abdomens missing from three. Three additional male syntypes in USNM.

coloradella Dietz, 1905: 6, **Amydria;** SYNTYPES (1 male, 3 females), MCZ 2902; United States: Arizona, Santa Rita Mountains; California, Kaweah; and Colorado, Durango; *Amydria effrentella* Clemens; Two additional (male, female) syntypes in USNM.

confusella Dietz, 1905: 8, **Amydria;** SYNTYPES (6 females), MCZ 2906; United States: California, Pasadena; Two additional female syntypes in USNM.

costotristgella Chambers, 1873a: 87, **Tinea;** SYNTYPE male, MCZ 14947; United States: Kentucky, August and September, Chambers; *Nemapogon granella* (Linnaeus); Specimen in poor condition; right forewing and abdomen missing. No other syntypes are known.

crescentella Kearfott, 1907b: 9, **Amydria;** SYNTYPE male, MCZ 14235; United States: Arizona, Pima County, Baboquivari Mountains; *Acrolophus crescentella* (Kearfott); Three additional male syntypes in USNM. Presumably the fifth remaining syntype is in University of Kansas collection, Lawrence, Kansas.

cristatella Chambers, 1875b: 243, **Semele;** SYNTYPE male, MCZ 1401; United States: Kentucky, June, Chambers; *Homosetia cristatella* (Chambers); No other syntypes known.

croceoverticella Chambers, 1876b: 106, **Tinea;** SYNTYPE male, MCZ 1393; United States: Kentucky, Chambers; No other syntypes known.

cruciferella Dietz, 1905: 14, **Paraneura;** SYNTYPES (2 males), MCZ 2895; United States: California, Mountain View; **Lindera tessellatella** (Blanchard); One male "cotype" each in LACM and USNM are pseudotypes.

curviliniella Dietz, 1905: 71, **Homostinea;** SYNTYPES (3 males), MCZ 2866; United States: District of Columbia, [Washington, A. Busck]; Kansas, Onaga; Louisiana, Vowells Mill; and, Missouri, St. Louis; Louisiana syntype is lost (only pin and labels remaining in MCZ). One male syntype (Washington, D.C.) is also present in LACM, but a second female "cotype" from Kentucky is a pseudotype.

curvistrigella Deitz, 1905: 8, **Amydria;** SYNTYPE female, MCZ 2905; United States: Arizona, Phoenix; Additional male syntype in USNM.

dyarella Dietz, 1905: 11, **Amydria;** HOLOTYPE female, MCZ 14234; United States: Pennsylvania, Hazleton; Two female paratypes also exist, one in MCZ and one in USNM.

ehrhornella Dietz, 1905: 13, **Paraneura;** SYNTYPES (2 males), MCZ 2894; United States: California, Mountain View; *Lindera tessellatella* (Blanchard).

cunitariaeella Chambers, 1873a: 85, **Tinea;** SYNTYPES (2 males, 2 females), MCZ 1398, United States: Kentucky, Chambers; *Eudarcia cunitariaeella* (Chambers).

fasciella Chambers, 1873a: 111, **Pitys;** SYNTYPE female, MCZ 1347; United States: Kentucky, Chambers; *Homosetia fasciella* (Chambers); No other syntypes are known. Another female in extremely worn condition bearing Chambers' Kentucky label exists in MCZ, but it shows no other indications of being a syntype.

floridella Dietz, 1905: 77, **Progona;** HOLOTYPE female, MCZ 2869; United States: Florida, Hastings; *Mea skinnerella* (Dietz). Holotype erroneously stated to be a male by Dietz.

fractiliniella Dietz, 1905: 17, **Apotomia;** SYNTYPE male, MCZ 2899, United States: California, Pasadena; *Setomorpha rutella* Zeller; Additional female syntype in USNM.

frigidella Packard, 1867: 62, **Oecophora;** SYNTYPES (2 females), MCZ 1549, Canada: Labrador, Caribou Island, Square Island; *Niditinea fuscella* (Linnaeus); Both syntypes in very poor condition with the abdomen missing from one.

fulvisuffusella Dietz, 1905: 68, **Tinea;** HOLOTYPE male, MCZ 2864, United States: New Hampshire, Hampton; *Nemapogon variatella* (Clemens); A male pseudotype from the same locality in USNM.

fuscocristatella Chambers, 1873a: 111, **Pitys;** SYNTYPE(S), presumed lost; United States: Kentucky; *Homosetia fuscocristatella* (Chambers); Dietz (1905) examined the "type" of this species in the MCZ and considered it a synonym of *Homosetia miscecristatella* Chambers.

fuscofasciella Chambers, 1875b: 257, **Euplocamus (?);** LECTOTYPE female, MCZ 1385; United States: Kentucky, Chambers; *Montescardia fuscofasciella* (Chambers); Lectotype designated by Robinson (1986: 76).

fuscomaculella Chambers, 1873a: 88, **Tinea;** SYNTYPE male, MCZ 14946; United States: Kentucky, Chambers; *Nemapogon granella* (Linnaeus); No other syntypes known.

geniculatella Dietz, 1905: 62, **Tinea;** SYNTYPES (2 females), MCZ 2861; United States: California, Occidental and Pasadena; *Nemapogon geniculatella* (Dietz); Deposition of an additional syntype from Kaweah, California, is unknown.

griseella Chambers, 1873a: 88, **Tinea;** SYNTYPES (2 males), MCZ 1389, United States: Kentucky, Chambers; *Niditinea fuscella* (Linnaeus); One syntype in very poor condition with head, abdomen, and left forewing missing.

hybromella Chambers, 1874a: 51, **Oenoe;** SYNTYPE [illegible] MCZ [illegible] United States: Kentucky, Chambers [illegible]

inamoenella Zeller, 1873: 224, **Setomorpha;** HOLOTYPE male, MCZ 2882; United States: Texas, Dallas, Boll; *Setomorpha rutella* Zeller.

interstitiella Dietz, 1905: 68, **Tinea;** HOLOTYPE male, MCZ 2865; United States: Georgia, Forsyth; *Nemapogon interstitiella* (Dietz).

irrorella Dietz, 1905: 34, **Monopis;** SYNTYPES (4 males, 3 females), MCZ 2872; United States: Pennsylvania, Hazleton and Mauch Chunk; *Monopis marginistrigella* (Chambers); Additional syntypes in LACM (1 male, 1 female) and USNM (2 males). Deposition of syntype(s) from New York unknown.

maculatella Dietz, 1905: 84, **Homosetia;** SYNTYPES (2 males), MCZ 2851; United States: California, Placer County; Pennsylvania, Hazleton; *Homosetia marginimaculella* (Chambers); Syntype from Placer County, California, missing abdomen.

majorella Dietz, 1905: 15, **Setomorpha;** SYNTYPES (2 females), MCZ 2896; United States: California, Pasadena; *Setomorpha rutella* Zeller.

marginistrigella Chambers, 1873a: 88, **Tinea;** SYNTYPE, MCZ 14950; United States: Kentucky, Chambers; *Monopis marginistrigella* (Chambers); Specimen in very poor condition, glued to a point with only the head, prothorax, and right forewing. No other syntypes known.

margoriella Dietz, 1905: 11, **Amydria;** SYNTYPES (4 males), MCZ 2891; United States: Florida; Kansas, Lawrence; Texas, San Antonio; The type series appears to be mixed, with the eastern records most likely representing *Amydria dyarella* Dietz. Dietz (1905) mentions syntypic material in USNM, but none has been found.

minutipulvella Chambers, 1875e: 212, **Tinea;** SYNTYPE female, MCZ 1390; Canada; *Nemapogon acapnopennella* (Clemens); Another female syntype in USNM.

miriamella Dietz, 1905: 90, **Leucomele;** SYNTYPES (4 males, 2 females), MCZ 2854; United States: Maryland, Plummer's [sic] Island; Pennsylvania, Hazleton and Mauch Chunk; Two additional male syntypes in USNM and one male syntype in BMNH.

miscecristatella Chambers, 1873a: 111, **Pitys;** SYNTYPE female, MCZ 1395; United States: Kentucky, Chambers; *Homosetia miscecristatella* (Chambers); No other syntypes known.

miscella Chambers, 1873a: 86, **Tinea;** SYNTYPE(S), presumed lost; United States: Kentucky; Dietz (1905) reported the poorly preserved "type" in MCZ.

molybdanella Dietz, 1905: 61, **Tinea**; SYNTYPES (2 females), MCZ 2880; United States: California, Pasadena; *Nemapogon molybdanella* (Dietz).

multimaculella Chambers, 1878e: 89, **Gelechia?;** SYNTYPES (2 males), MCZ 1451; United States: Texas; *Setomorpha rutella* Zeller.

multistriatella Dietz, 1905: 59, **Tinea**; SYNTYPES (2 females), MCZ 2878; [Canada: Toronto]; *Nemapogon multistriatella* (Dietz); A female syntype is also present in the LACM (Plummers Island, Maryland). The MCZ syntypes lack locality labels.

nepotella Dietz, 1905: 21, **Epichaeta;** SYNTYPES (2 females), MCZ 2887; United States: California, Pasadena; *Apreta paradoxella* Dietz.

nigroatomella Dietz, 1905: 70, **Tinea;** HOLOTYPE, MCZ 2865; United States: New Jersey, Montclair, W. D. Kearfott; *Nemapogon granella* (Linnaeus).

obliquella Dietz, 1905: 10, **Amydria;** SYNTYPES (2 females), MCZ 2909; United States: California, Los Angeles County, Pasadena; Additional male syntype (Los Angeles County) in USNM.

obscurella Dietz, 1905: 82, **Homosetia;** HOLOTYPE male, MCZ 14945; United States: Kansas, Onaga; *Homosetia bifasciella* (Chambers).

occidentella Dietz, 1905: 9, **Amydria onagella;** SYNTYPES, presumed lost; United States: California, Mountain View and Pasadena.

occidentella Chambers, 1880b: 193, **Tinea tapetzella;** SYNTYPES (1 male, 1 female?), MCZ 1392; United States: California, San Francisco; *Tinea occidentella* Chambers; According to Chambers, the type series consisted of three specimens. The location of the third syntype is unknown.

onagella Dietz, 1905: 9, **Amydria;** SYNTYPES (2 males), MCZ 2908; United States: Kansas, Onaga; One syntype missing right wings.

operosella Zeller, 1873: 223, **Setomorpha;** HOLOTYPE male, MCZ 2881; United States: Texas, Dallas, Boll; *Setomorpha rutella* Zeller; Abdomen and left wings missing.

ophrionella Dietz, 1905: 56, **Tinea;** HOLOTYPE male, MCZ 2875; United States: New York, Ithaca; *Nemapogon ophrionella* (Dietz); Left wings missing.

orleansella Chambers, 1873a: 85, **Tinea;** SYNTYPE male, MCZ 14949; United States: Louisiana, New Orleans; *Niditinea orleansella* (Chambers); Syntype in poor condition, unspread, and glued to a point. No other syntypes known.

pandurella Dietz, 1905: 8, **Amydria;** SYNTYPES (2 males), MCZ 2907; United States: Arizona, Phoenix; California, Pasadena; *Amydria curvistrigella* Dietz; Dietz stated that the type series consisted of "two specimens, [male] and [female], in my collection." A second specimen in MCZ is hereby considered a syntype even though it is also a male (i.e., sex misdetermined by Dietz) and bears no type labels. Two "cotypes" in USNM must thereby be regarded as pseudotypes. One of these (from Pasadena) is a female, but it was misidentified and is *A. confusella* Dietz.

paradoxella Dietz, 1905: 21, **Apreta;** HOLOTYPE female, MCZ 2186; United States: California, Pasadena; Dietz (1905) misdetermined the holotype as a male.

rileyi Dietz, 1905: 59, **Tinea;** SYNTYPES (3 females), MCZ 2879; United States: Pennsylvania, Hazleton; District of Columbia; Florida Hastings; *Nemapogon rileyi* (Dietz); One female syntype collected by Busck in Washington, D.C., and loaned to Dietz has been returned to USNM. The 25 specimens from Hastings, Florida (reared by Riley) were referred to by Dietz in the original description.

roburella Dietz, 1905: 58, **Tinea;** HOLOTYPE male, MCZ 2877; United States: New Jersey, Essex County [Park], W. D. Kearfott; *Nemapogon roburella* (Dietz).

ruderella Zeller, 1873: 225, **Setomorpha;** HOLOTYPE male, MCZ 14233; United States: Texas, Dallas, Boll; *Setomorpha rutella* Zeller.

scardina Zeller, 1873: 215, **Anaphora;** SYNTYPES (2 males), MCZ 33318; United States: Texas, Dallas, Boll; *Acrolophus popeanella* (Clemens); Two additional male syntypes in BMNH ("Carolina" and Texas).

septemstrigella Chambers, 1878c: 79, **Tinea;** HOLOTYPE male, MCZ 1386; United States: Texas; *Augolychna septemstrigella* (Chambers).

sepulchrella Dietz, 1905: 74, **Tryptodema;** SYNTYPE male, MCZ 2867; United States: Maryland, Plummer's [sic] Island, A. Busck; Three additional syntypes (2 males, 1 female) in USNM.

sigmoidella Dietz, 1905: 16, **Setomorpha;** SYNTYPES (2 males), MCZ 2897; United States: Colorado, Glenwood Springs, Pueblo; *Setomorpha rutella* Zeller; One additional male syntype each in USNM and LACM.

simulella Dietz, 1905: 13, **Paraneura;** SYNTYPE female, MCZ 2893; United States: California, Folsom and Los Angeles; *Lindera tessellatella* Blanchard; A second syntype (Los Angeles) in LACM.

skinnerella Dietz, 1905: 76, **Progona;** HOLOTYPE male, MCZ 2868; United States: New Jersey, Caldwell; *Mea skinnerella* (Dietz).

straminiella Chambers, 1873a: 86, **Tinea;** SYNTYPE(S), presumed lost; United States: Kentucky, June.

texanella Chambers, 1878c: 79, **Anaphora;** SYNTYPE male, MCZ 1383; United States: Texas; *Acrolophus texanella* (Chambers); No other syntypes known.

thoracestrigella Chambers, 1876b: 106, **Tinea;** SYNTYPE(S), presumed lost; United States: [type locality not stated].

transversestrigella Dietz, 1905: 20, **Semiota;** SYNTYPES (8 males), MCZ 2900; United States: Cali-

fornia, Pasadena, *Setomorpha rutella* Zeller; Four additional male syntypes in USNM.

tuscanella Dietz, 1905: 53, **Tinea:** SYNTYPE female, MCZ 2884; United States: Arizona, Tuscan [Tucson]; *Tinea occidentella* Chambers; No other syntypes known.

unomaculella Chambers, 1875b: 258, **Tinea:** SYNTYPE female, MCZ 1387; United States: Texas; No other syntypes known.

vicinella Dietz, 1905: 55, **Tinea:** HOLOTYPE female, MCZ 2885; United States: Florida, Gotha; *Ceratophaga vicinella* (Dietz); Sex given as male in original description.

visaliella Chambers, 1873a: 113, **Cyane:** SYNTYPE male, MCZ 14974; United States: Kentucky, Visalia, Chambers; *Choropleca visaliella* (Chambers); The single known syntype is badly broken with the remaining parts glued to a point.

xanthostictella Dietz, 1905: 56, **Tinea:** HOLOTYPE male, MCZ 2876; United States: Georgia, Forsyth.

yumaella Kearfott, 1907b: 6, **Plutella:** SYNTYPE male (1 of 16), MCZ 11858; United States: Arizona, Yuma County, Desert; *Dyotopasta yumaella* (Kearfott); Nine Yuma County syntypes in USNM, some of the remaining syntypes (other localities) at University of Kansas.

Family Lyonetiidae

albella Chambers, 1871a: 23, **Cemiostoma:** SYNTYPES (2 of 4), MCZ 1306; United States: Kentucky, Chambers, *Paraleucoptera albella* (Chambers); One possible syntype in USNM (type 518).

albella Chambers, 1877d: 140, **Eurynome:** SYNTYPES (2), MCZ 1312; United States: Colorado, near Edgerton, elevation about 6,500 feet; *Philonome albella* (Chambers); Two possible syntypes in LACM.

albicapitella Chambers, 1875e: 125, **Bucculatrix:** SYNTYPE (?), MCZ 14962; Canada; *Bucculatrix agnella* Chambers, Missing hind wings and abdomen. Braun (1963: 79) considered this name "an apparent transposition of syllables" of *capitealbella* Chambers. One possible syntype in USNM (type 5776).

alniella Chambers, 1875e: 303, **Lyonetia:** SYNTYPES (9), MCZ 1313, United States: Colorado, "along Grand River, Clear Creek, Fall River and Fontain-qui-Bouille, in all its stages, up to 9,000 feet altitude". Another syntype in LACM.

ambrosiaefoliella Chambers, 1875a: 119, **Bucculatrix:** SYNTYPES (2), MCZ 1308, United States: Kentucky, bred from leaves of *Ambrosia trifida* Linnaeus, Chambers.

apicistrigella Chambers, 1875a: 105, **Lyonetia;** SYNTYPE, MCZ 1314; United States: Kentucky, August, Chambers; *Lyonetia speculella* Clemens; Missing abdomen.

canadensisella Chambers, 1875e: 146, **Bucculatrix;** SYNTYPE, MCZ 1307; Canada; Missing abdomen. According to Braun (1963: 147) there is a female type in USNM (type 5775), but we could not locate it.

capitealbella Chambers, 1873a: 150, **Bucculatrix;** HOLOTYPE, MCZ 14961; United States: Kentucky, Chambers; *Bucculatrix agnella* Clemens; One "syntype" in USNM (type 519).

clemensella Chambers, 1874a: 97, **Philonome;** SYNTYPES 7 (2 missing from pins), MCZ 1311; United States: Kentucky, Chambers; One possible syntype in USNM (type 522).

curvilineatella Packard, 1869: 354, pl. 8, fig. 16, **Lithocolletis:** SYNTYPE, MCZ 1347; [United States]; *Bucculatrix pomifoliella* Clemens; Broken and missing head.

fuscoscapulella Chambers, 1878c: 104, **Acanthocnemes;** SYNTYPE, MCZ 1530; United States: Texas, Bosque County; Missing head and forewings.

inornatella Chambers, 1880b: 188, **Eulyonetia;** SYNTYPE, MCZ 1353; United States: Texas, Belfrage; Missing left wings and abdomen.

litigiosella Zeller, 1875: 354, **Bucculatrix:** SYNTYPE (1 of 2) female (not male as stated by Zeller), MCZ 14959; United States: Texas, Dallas, Boll.

luteella Chambers, 1873a: 151, **Bucculatrix;** SYNTYPES (7), MCZ 1501; United States: Kentucky, March, Chambers; Braun (1963: 153) stated that some of these syntypes are *Bucculatrix packardella*, and that there is a female syntype at USNM (type 520) and male syntype at ANSP.

luteella Chambers, 1875c: 304, **Eurynome;** HOLOTYPE, MCZ 14964; United States: Colorado, Spanish Bar, 4 July; *Philonome luteella* (Chambers).

magnella Chambers, 1875d: 54, **Bucculatrix;** SYNTYPES (6), MCZ 1309; United States: Kentucky, Chambers; Braun (1963: 42-43) listed only one female "type" in MCZ, and two "paratypes" in USNM.

obscurofasciella Chambers, 1873a: 150, **Bucculatrix;** SYNTYPE female, MCZ 1500; United States: Kentucky, 23 May, Chambers; *Bucculatrix trifasciella* Clemens; Braun (1963: 136–137) noted a female syntype in USNM (type 521).

packardella Chambers, 1873a: 151, **Bucculatrix;** "SYNTYPES" (2), MCZ 14960; United States: Kentucky, Chambers; Two specimens glued to the same point, labelled only "Kentucky, Chambers." and

"Type/14960." Braun (1963: 129) stated "Two specimens thus named, presumably by Chambers, in the Museum of Comparative Zoology, but not labeled types, do not represent this species."

staintonella Chambers, 1878d: 133, **Bucculatrix;** LECTOTYPE male, MCZ 1310; United States: Colorado, Edgerton, elevation 6,000 feet; Originally described by Chambers (1877d: 141) as *B. albella*, a name preoccupied by Stainton. Lectotype designated by Braun (1963: 74).

SUPERFAMILY GELECHIOIDEA

Family Oecophoridae

[Note: The Walsingham syntypes listed below were received by Chambers from Walsingham. Lectotypes should be designated from BMNH specimens.]

albaciliaeella Chambers, 1878b: 77, **Strobisia;** HOLOTYPE, MCZ 1548; United States: Ohio, Cincinnati; *Menesta tortriciformella* Clemens; Head and thorax only.

albella Chambers, 1874b: 235, **Harpalyce;** SYNTYPES (5), MCZ 1417; United States: Texas, Clifton, Belfrage; *Durrantia piperatella* (Zeller).

apicipunctella Chambers, 1875d: 8, **Hyponomeuta;** LECTOTYPE male, MCZ 1404; United States: Texas, Basque [sic] County, Belfrage; *Ethmia apicipunctella* (Chambers); Lectotype designated by Powell (1973: 88), also paralectotype in MCZ.

argillacea Walsingham, 1881: 313, pl. XXXVI, fig. 2, **Depressaria;**; SYNTYPE, MCZ 14975; United States: California, Tehama County, Newville; *Agonopterix argillacea* (Walsingham).

arnicella Walsingham, 1881: 314, pl. XXXVI, fig. 3, **Depressaria;**; SYNTYPE, MCZ 14976; United States: California, Mount Shasta; *Agonopterix arnicella* (Walsingham).

bicostomaculella Chambers, 1877a: 127, Gelechia; SYNTYPE male, MCZ 1461; United States: Colorado, Edgerton, July; *Taygete decemmaculella* (Chambers); Hodges (1986: 6) transferred *decemmaculella* to Oecophoridae.

boreasella Chambers, 1873a: 189, **Oecophora;** LECTOTYPE male, MCZ 1553; United States: Kentucky; *Decantha boreasella* (Chambers); Lectotype designated by Hodges (1974: 104).

canusella Chambers, 1874b: 235, **Harpalyce;** SYNTYPE, MCZ 1415; United States: Texas, [13/8]; *Antaeotricha humilis* (Zeller).

chrysurella Dietz, 1905: 42, **Breckenridgia** [sic]; HOLOTYPE male, MCZ 33274; United States: [Southwest] Colorado, ["6-28-89"]; *Ethmia albistrigella* (Walsingham).

clemensella Chambers, 1876b: 173, **Gelechia;** SYNTYPES (5), MCZ 1488; United States: Pennsylvania, Easton; *Agonopterix clemensella* (Chambers).

coryliella Chambers, 1875b: 242, **Hyale;** SYNTYPE, MCZ 14974; United States: Kentucky, Covington, Chambers; *Menesta tortriciformella* Clemens.

cressonella Chambers, 1878c: 86, **Cryptolechia;** LECTOTYPE male, MCZ 1420; United States: Texas; *Psilocorsis cryptolechiella* (Chambers); Lectotype designated by Hodges (1974: 92), also 2 paralectotypes in MCZ.

difficilisella Chambers, 1872a: 66, **Evagora;** SYNTYPE male, MCZ 1528; United States: Kentucky, Chambers; *Taygete attributella* (Walker); Hodges (1986: 6) transferred *attributella* to Oecophoridae.

discostrigella Chambers, 1877d: 122, **Anesychia;** LECTOTYPE male, MCZ 1421; United States: Colorado, Edgerton, 6,500 feet; *Ethmia discostrigella* (Chambers); Lectotype designated by Powell (1973: 93), also 4 paralectotypes in MCZ.

eupatoriiella Chambers, 1878c: 82, **Depressaria;** SYNTYPE, MCZ 1432; United States: Kentucky, Chambers; *Agonopterix eupatoriiella* (Chambers).

faginella Chambers, 1872a: 131, **Hagno;** LECTOTYPE male, MCZ 1419; United States: Kentucky, Chambers; *Psilocorsis cryptolechiella* (Chambers); Lectotype designated by Hodges (1974: 92), also 4 paralectotypes in MCZ.

fernaldella Chambers, 1878c: 82, **Depressaria;** Possible SYNTYPES (2); United States: Maine; *Machimia tentoriferella* Clemens; Two specimens with no type labels may be types: one is labelled "Me"; "47" [pencil]; "fernaldella/Chb" [Chambers' pen]; "Machimia/(tentoriferella?)/AB May 1900"; the other "L.I." [?, pencil, illegible]; "Kentucky.[crossed out]/Chambers."; "22" [Chambers' hand].

fernaldella Riley, 1889: 155, **Setiostoma;** SYNTYPES (2 of 12), MCZ 11907; United States: California, Los Angeles County; Other syntypes in USNM; Lectotype should be designated from USNM specimen.

hagenella Chambers, 1878c: 80, **Anesychia;** LECTOTYPE male, MCZ 1422; United States: Texas, Bosque County; *Ethmia hagenella* (Chambers); Lectotype designated by Powell (1973: 110), also paralectotype in MCZ.

lithosina Zeller, 1873: 244, **Cryptolechia;** HOLOTYPE male, MCZ 1717; United States: Texas, Dallas, Boll; *Antaeotricha unipunctella* (Clemens).

longimaculella Chambers, 1872a: 43, **Hyponomeuta;** LECTOTYPE male, MCZ 1403; United States: Kentucky, Chambers; *Ethmia longimaculella* (Chambers); Lectotype designated by Powell (1973: 178), also 4 paralectotypes in MCZ.

mirusella Chambers, 1874b: 233, **Anesychia;** LECTOTYPE male, MCZ 1423; United States: Texas, Belfrage; *Ethmia mirusella* (Chambers); Lectotype designated by Powell (1973: 193), also 4 paralectotypes in MCZ.

multipunctella Chambers, 1874b: 233, **Anesychia;** LECTOTYPE male, MCZ 1425; United States: Texas, Waco, Belfrage; *Ethmia semilugens* (Zeller). Lectotype designated by Powell (1973: 86), also 13 paralectotypes in MCZ.

nebeculosa Zeller, 1873: 245, fig. 12, **Cryptolechia;** SYNTYPES (4), MCZ 1720; United States: Texas, Dallas, Boll; *Antaeotricha humilis* (Zeller).

novi-mundi Walsingham, 1881: 318, **Depressaria;** SYNTYPE, MCZ 14971; United States: California and Oregon; *Exaeretia thoracenigraeella* (Chambers).

nubiferella Walsingham, 1881: 316, pl. XXXVI, fig. 6, **Depressaria;** SYNTYPE, MCZ 14977; United States, Oregon, Rogue River; *Agonopterix nubiferella* (Walsingham).

obscuromaculella Chambers, 1878c: 86, **Cryptolechia?;** SYNTYPE, MCZ 1418; United States: Texas, Bosque County, [11 8.]; *Inga obscuromaculella* (Chambers); Another syntype in USNM (Hodges, 1974: 102).

piperatella Zeller, 1873: 239, **Cryptolechia;** HOLOTYPE male, MCZ 1719; United States: Texas, Dallas, Boll; *Durrantia piperatella* (Zeller).

posticella Walsingham, 1881: 315, pl. XXXVI, fig. 5, **Depressaria;** SYNTYPE, MCZ 14972; United States: California and Oregon; *Agonopterix posticella* (Walsingham).

quinqueferella Walsingham, 1881: 322, **Glyphipteryx** [sic]; PARALECTOTYPE (?), MCZ [no number], United States: [California]; *Fabiola quinqueferella* (Walsingham). Designated a paralectotype by Heppner (1978: 49), but, as noted by Heppner (1984: 338), it might not be one of the original syntypes.

shaleriella Chambers, 1875a: 114, **Oecophora;** SYNTYPE, MCZ 1552, United States: Kentucky, Chambers, *Fabiola shaleriella* (Chambers); Head and thorax only.

texanella Chambers, 1880b: 180, **Hyponomeuta;** LECTOTYPE, MCZ 1406, United States, Texas; *Ethmia zelleriella* (Chambers). Lectotype designated by Powell (1973: 113).

thoracefasciella Chambers, 1875b: 246, **Gelechia;** SYNTYPE, MCZ 1465, United States: California, *Exaeretia thoracefasciella* (Chambers).

thoracenigraeella Chambers, 1875b: 246, **Gelechia;** SYNTYPE, MCZ 1466; United States, California; *Exaeretia thoracenigraeella* (Chambers). Fragment in capsule.

tortricella Chambers, 1874b: 235, **Harpalyce;** SYNTYPES (3), MCZ 1416; United States: Texas; *Antaeotricha unipunctella* (Clemens).

trifurcella Chambers, 1873: 12, **Anesychia;** LECTOTYPE female, MCZ 1426; United States: Kentucky, Chambers; *Ethmia trifurcella* (Chambers); Lectotype designated by Powell (1973: 194).

umbraticostella Walsingham, 1881: 318, pl. XXXVI, fig. 8,; **Depressaria;** SYNTYPE, MCZ 14973; United States: California and Oregon; *Exaeretia umbraticostella* (Walsingham).

vestalis Zeller, 1873: 247, **Cryptolechia;** HOLOTYPE female, MCZ 1718; United States: Texas, Dallas, Boll; *Antaeotricha vestalis* (Zeller).

xanthobasis Zeller, 1875: 324, **Setiostoma;** HOLOTYPE male, MCZ 33256; United States: Texas, Dallas, Boll; *Rectiostoma xanthobasis* (Zeller).

zelleriella Chambers, 1878c: 80, **Hyponomeuta;** LECTOTYPE female, MCZ 1405; United States: Texas, Bosque County; *Ethmia zelleriella* (Chambers); Lectotype designated by Powell (1973: 113).

Family Elachistidae

parvipulvella Chambers, 1875d: 56, **Elachista;** PSEUDOTYPES (4), MCZ 1513; United States: Texas; Braun (1948: 51) stated that none of the 4 MCZ specimens is an *Elachista* and that the real type is in USNM.

staintonella Chambers, 1878c: 96, **Elachista;** SYNTYPE male, MCZ 1514; United States: Texas.

Family Blastobasidae
David Adamski

ampla Dietz, 1900a: 103, pl. VI, fig. 1, **Ploiophora;** SYNTYPES (4 males), MCZ 2923; Adamski gen. slide nos. 2159, 2160, 2161; United States: Pennsylvania, Hazleton; 1 syntype missing abdomen; 1 male erroneously labeled as "type" (no. 6135) in USNM (Adamski gen. slide no. 2471).

angustipennella Dietz, 1900a: 108, **Pigritia;** SYNTYPES (5), MCZ 2930; Adamski gen. slide nos. 2166 (male), 2167; (male), 2168 (female); 1 syntype missing abdomen; 1 syntype not dissected; United States: Pennsylvania, Hazleton; 1 male erroneously labeled as "type" (no. 6157) in USNM (Adamski gen. slide no. 2473).

annectella Dietz, 1910: 63, pl. IV, fig. 34a, **Holcocera zelleriella** var.; SYNTYPES (2 females of 3), MCZ 2932; Adamski gen. slide nos. 2150, 2151; United States, Iowa, Iowa City; Louisiana, Vowell's Mill; 1 syntype lost.

annulipes Dietz, 1910: 58, **Holcocera crescentella** var.; HOLOTYPE female, MCZ 2950; United States:

Arizona, Bahoyquivaria [sic] Mountains; Abdomen missing.

argyreella Dietz, 1900a: 113, **Pseudopigritia;** HOLOTYPE male, MCZ 2920; Adamski gen. slide no. 2201; United States: Pennsylvania, Hazleton.

argyrosplendella Dietz, 1910: 22, pl. II, figs. 13, 13a, 13b, **Calosima:** SYNTYPES (3 of 3), MCZ 2968, 1 male, 1 female; Adamski gen. slide nos. 2059, 2060; United States: Pennsylvania, Hazleton; Florida, Hastings; Louisiana, Vowells Mill; Syntype from Louisiana missing abdomen.

arizonella Dietz, 1900a: 109, **Pigritia;** SYNTYPES (2 of 2 males), MCZ 2912; Adamski gen. slide nos. 2169, 2170; United States: Arizona, Huachuca, and Nochales [sic].

aufugella Zeller, 1873: 301, **Blastobasis;** HOLOTYPE, MCZ 14978; United States: Texas, [Dallas], Boll; *Pigritia laticapitella* Clemens; Abdomen missing.

basilarella Dietz, 1900a: 105, pl. VI, fig. 6, **Pigritia;** SYNTYPES (3 of 3), MCZ 2928; Adamski gen. slide no. 2171 (female); United States: Pennsylvania, Hazleton; Kansas, Lawrence; Iowa; 2 syntypes missing abdomens.

basipallidella Dietz, 1910: 26, **Holcocera dives** var.; SYNTYPES (2 of 3), MCZ 2951, 1 male and 1 female; Adamski gen. slide nos. 2082, 2085; United States: Pennsylvania, Hazleton; New Hampshire, Hampton; 1 syntype from Cohasset, Massachusetts in USNM (Adamski gen. slide no. 2434 — male).

boreasella Dietz, 1910: 47, pl. III, fig. 22, **Holcocera;** SYNTYPES (4 of 5), MCZ 2960, females; Adamski gen. slide nos. 2064, 2065, 2066; R. B. Selander gen. slide no. 701; United States: New Hampshire, Webster; Canada: Montreal; 1 syntype lost.

busckiella Dietz, 1910: 36, pl. II, fig. 19, **Holcocera;** SYNTYPES (2 males of 7), MCZ 2956; Adamski gen. slide nos. 2067, 2068; United States: Maryland, Plummer's [sic] Island, July and August 1903, A. Busck; 5 syntypes in USNM; 1 male dissected (Adamski gen. slide no. 2424), 4 without abdomens.

canariella Dietz, 1900a: 118, pl. VII, fig. 17, **Dryope;** HOLOTYPE, male, MCZ 14226; Adamski gen. slide no. 2212; United States: California, Sonoma County; *Dryoperia canariella* (Dietz).

confectella Zeller, 1873: 303, **Hypatima;** HOLOTYPE female, MCZ 2083; United States: Texas, [Dallas], Boll; *Valentinia confectella* (Zeller); Abdomen missing.

confluentella Dietz, 1910: 36, pl. II, fig. 18, **Holcocera;** SYNTYPES (2 of 4), MCZ 2955, female; Adamski gen. slide no. 2156; 1 syntype missing abdomen; United States: Pennsylvania, Hazleton; Central New York; *Holcocerina confluentella* (Dietz); 1 syntype from Cohasset, Massachusetts, in USNM (Adamski gen. slide no. 2429 — female). 1 syntype lost.

confusella Dietz, 1900a: 104, pl. VI, fig. 4, **Pigritia;** SYNTYPES (4), MCZ 2925; Adamski gen. slide nos. 2172 (female), 2173 (male), 2174 (female); 1 syntype not dissected; United States: Pennsylvania, [Hazleton]; 1 syntype from [Montclair], New Jersey, in USNM (type no. 6131) (Adamski gen. slide no. 2476 — female).

crescentella Dietz, 1910: 57, pl. IV, fig. 31, **Holcocera;** HOLOTYPE female, MCZ 2949; Adamski gen. slide no. 2081; United States: Utah, Stockton, T. Spalding.

dianella Dietz, 1910: 22, **Calosima;** HOLOTYPE male, MCZ 2969; Adamski gen. slide no. 2061; United States: Georgia, Forsyth, 1895.

discopunctella Dietz, 1900a: 118, pl. VII, fig. 16, **Dryope;** HOLOTYPE female, MCZ 14223; Adamski gen. slide no. 2213; United States: Pennsylvania, Hazleton; *Dryoperia discopunctella* (Dietz).

dives Dietz, 1910: 26, pl. II, fig. 14 (male), **Holcocera;** SYNTYPES (2 of 7), MCZ 2951, females; Adamski gen. slide nos. 2083, 2084; United States: Pennsylvania, Hazleton; Maryland, Plummer's [sic] Island; Canada: Toronto; 3 syntypes from Charleroi, Pennsylvania in USNM (Adamski gen. slide nos. 2431, 2433 (females) and 2432 (male)). 1 syntype lost.

dorsomaculella Dietz, 1900a: 112, pl. VII, fig. 10, **Pseudopigritia;** SYNTYPES (2 of 2), MCZ 2917, male and female, both specimens missing abdomens; United States: Pennsylvania, Hazleton.

elyella Dietz, 1910: 49, pl. III, fig. 25, **Holcocera;** SYNTYPES (7 of 17), MCZ 2941; Adamski gen. slide nos. 2086 (female), 2087 (male), 2088 (male), 2089 (female); United States: Connecticut, East River, C. R. Ely; Maryland, Plummer's [sic] Island, A. Busck, and Frederick; New Jersey, Essex County, W. D. Kearfott; Specimens comprising remainder of original syntype series cannot be determined.

equitella Dietz, 1900a: 112, **Pseudopigritia;** SYNTYPES (3 females), MCZ 2918; Adamski gen. slide nos. 2204, 2205; 1 syntype missing adbomen; United States: Pennsylvania, Hazleton.

estriatella Dietz, 1910: 28, pl. II, fig. 15, **Holcocera;** HOLOTYPE male, MCZ 2970; Adamski gen. slide no. 2090; United States: Massachusetts, [Cohasset].

fenyesella Dietz, 1900a: 119, **Dryope;** HOLOTYPE male, MCZ 14224; Adamski gen. slide no. 2214; United States: California, Pomona, A. Fenyes; *Dryoperia fenyesella* (Dietz).

fidella Dietz, 1900a: 103, pl. VI, figs. 2, 2a (male), 2b (female), 2c (male), **Ploiophora;** SYNTYPES (5), MCZ 2924; Adamski gen. slide nos. 2162 (male),

2163 (female), 2164 (female); two syntypes not dissected; United States: Pennsylvania, Hazleton; 1 syntype and 1 specimen erroneously labeled as "type" (type no. 6126) in USNM (Adamski gen. slide nos. 2472, 2473 — males).

floridella Dietz, 1910: 17, pl. I, fig. 10, **Valentinia;** SYNTYPES (1 of 4), MCZ 2966, female (no abdomen); United States: Florida, Cresent City, [male] cone of *Zamia integrifolia*; 3 syntypes (male and 2 females) in USNM, 1 dissected (Adamski gen. slide no. 2415 — male); 1 male erroneously labeled as "cotype," MCZ 2966, from Florida, G. D. Hulst Collection.

fluxella Zeller, 1873: 301, **Blastobasis;** HOLOTYPE male, MCZ 1711; Adamski gen. slide no. 2091; United States: Texas, [Dallas], Boll; *Holcocera fluxella* (Zeller).

fraternella Dietz, 1900a: 113, pl. VII, fig. 11, **Pseudopigritia;** HOLOTYPE male, MCZ 2919; Adamski gen. slide no. 2207; United States: Pennsylvania, Hazleton.

fumerella Dietz, 1910: 35, **Holcocera chalcofrontella** var.; SYNTYPES (6), MCZ 2954, females; Adamski gen. slide nos. 2074, 2075, 2076; 3 specimens not dissected.; United States: [Pennsylvania, Hazleton], bred from fruit racemes of sumach.

funebra Dietz, 1910: 44, **Holcocera;** SYNTYPES (2 of 5), MCZ 2092, Adamski gen. slide no. 2092 (male); United States: Maryland, Plummer's [sic] Island, 1903, A. Busck; Pennsylvania, Hazleton; 3 syntypes from Plummer's [sic] Island, Maryland in USNM (not dissected).

fuscopurpurella Dietz, 1910: 9, **Blastobasis plummerella** var.; HOLOTYPE female, MCZ 2962; Adamski gen. slide no. 2962; United States: Maryland, Plummer's [sic] Island; *Blastobasis plummerella* Dietz.

fuscosuffusella Dietz, 1900a: 117, pl. VII, fig. 13, **Dryope;** SYNTYPES (2 of 2), MCZ 14222, male and female; Adamski gen. slide nos. 2215, 2216; United States: Missouri, St. Louis; *Dryoperia fuscosuffusella* (Dietz).

gigantella Chambers, 1876b: 219, **Blastobasis;** LECTOTYPE male, MCZ 1551, J. A. Powell gen. slide no. 1008, United States: Colorado; *Holcocera gigantella* (Chambers); Lectotype and 3 paralectotypes in MCZ designated by Powell (1976). One other specimen from Colorado is at MCZ, may not be part of original series.

grisella Dietz, 1900a: 116, pl. VII, figs. 12, 12a, 12b (male), 12c (female), **Dryope;** SYNTYPE male, MCZ 14225; Adamski gen. slide no. 2218; United States: Pennsylvania, Hazleton; Missouri, Saint Louis; *Dryoperia grisella* (Dietz). At least 1 syntype lost. 1 syntype from collection of C. V. Riley in USNM (no. 743).

heidemanuella Dietz, 1900a: 111, pl. VII, fig. 9, **Epigritia;** SYNTYPES (2 of 7), MCZ 2916, females; Adamski gen. slide no. 2208; 1 syntype missing left hindwing, right forewing, and abdomen; United States: Pennsylvania, Bedford County, Sulfur Springs, on *Abies excelsa*, O. Heidemann; Epigritia ochrocomella (Clemens); 1 syntype in USNM (type no. 6133) (Adamski gen. slide no. 2483 — male); 4 syntypes lost.

hulstella Dietz, 1910: 7, pl. I, fig. 2, **Blastobasis;** HOLOTYPE female, MCZ 2977; Adamski gen. slide no. 2042; United States: Texas, G. Hulst.

iceryaeella Riley, 1887: 485, **Blastobasis;** SYNTYPES (4?), possible syntypes in MCZ; Adamski gen. slide nos. 2097, 2098 (1 male, 1 female); United States: California, Los Angeles County, Pasadena; *Holcocera iceryaeella* (Riley); At least 1 syntype from Alameda Co. and Los Angeles Co., California in USNM.

illibella Dietz, 1910: 57, pl. III, fig. 30, **Holcocera;** SYNTYPES (3 of 3), MCZ 2948, 2 males; Adamski gen. slide nos. 2101, 2102; United States: Maryland, Frederick; 1 syntype missing abdomen.

inclusa Dietz, 1910: 51, pl. III, fig. 27, **Holcocera;** HOLOTYPE male, MCZ 2943; Adamski gen. slide no. 2103; United States: Pennsylvania, Hazleton, 20 July 1904.

insulatella Dietz, 1910: 50, pl. III, fig. 26, **Holcocera;** SYNTYPES (2 of 2 males), MCZ 2942; Adamski gen. slide nos. 2104, 2105; United States: Colorado, Glenwood Springs, August.

interpunctella Dietz, 1910: 67, pl. IV, fig. 39, **Holcocera;** SYNTYPES (3 of 3), MCZ 2938, 2 males, 1 female; Adamski gen. slide nos. 2107, 2108, 2909; United States: Utah, Stockton, T. Spalding.

livorella Zeller, 1873: 299, **Blastobasis;** HOLOTYPE male, MCZ 2082; Adamski gen. slide no. 2110; United States: Texas, [Dallas], Boll; *Holcocera livorella* (Zeller).

luteopulvella Chambers, 1875d: 73, **Dryope;** SYNTYPE female, MCZ 1438; Adamski gen. slide no. 2178; United States: Kentucky, Chambers; *Pigritia laticapitella* Clemens.

mediofasciella Dietz, 1900a: 107, pl VI, fig. 5, **Pigritia;** HOLOTYPE female, MCZ 2927; Adamski gen. slide no. 2179; United States: [Pennsylvania, Hazleton], July.

melanostriatella Dietz, 1910: 66, pl. IV, fig. 38, **Holcocera;** SYNTYPES (7 of 9), MCZ 2937, 2 males; Adamski gen. slide nos. 2111, 2112; 5 syntypes missing abdomens; United States: Pennsylvania, Hazleton; Connecticut, East River, C. R. Ely; Maryland, Frederick; 2 syntypes from Frederick, Maryland, and East River, Connecticut, are lost.

messelinella Dietz, 1910: 52, pl. III, fig. 29, **Holco-**

cera; SYNTYPES (2 of 2 males), MCZ 2945; Adamski gen. slide nos. 2115, 2116; United States: Maryland, Frederick; Florida, Hastings.

minnicella Dietz, 1900a: 116, pl. VII, fig. 15, **Dryope;** SYNTYPES (5 of 5), MCZ 14221; Adamski male gen. slide nos. 2229, 2230 (3 syntypes not dissected); United States: Georgia, Forsyth; *Dryoperia minnicella* (Dietz); 1 syntype without "cotype" label, or lost.

minorella Dietz, 1910: 34, pl. II, fig. 17e, **Holcocera chalcofrontella** var.; SYNTYPES (4 of 6), MCZ 2953, female; Adamski gen. slide no. 2077; 3 syntypes not disseeted; United States: Pennsylvania, Lewisburg, Chestnut burrs; 2 syntypes lost.

murtfeldtella Chambers, 1874a: 50, **Dryope;** SYNTYPES (14), MCZ 1437; Adamski gen. slide nos. 2234 (male), 2235 (female); 8 syntypes with damaged or missing abdomens; 4 syntypes not dissected; United States: Kentucky; *Dryoperia murtfeldtella* (Chambers).

nubilella Zeller, 1873: 297, fig. 36, **Blastobasis;** HOLOTYPE female, MCZ 1714; Adamski gen. slide no. 2054; United States: Texas, [Dallas]; *Valentinia glandulella* (Riley).

obscurella Dietz, 1900a: 110, **Pigritia;** SYNTYPES (2 of 2), MCZ 2914; Adamski gen. slide no. 2180 (male); 1 syntype missing abdomen; United States: Pennsylvania, Hazleton.

occidentella Dietz, 1900a: 115, pl. VII, fig. 14, **Dryope;** HOLOTYPE female, MCZ 11300; United States: California, Kaweah; *Dryoperia occidentella* (Dietz); Missing left forewing and abdomen.

ochrocephala Dietz, 1910: 31, **Holcocera;** POSSIBLE SYNTYPE male, MCZ 2952; Adamski gen. slide no. 2123; United States: Maryland, [Plummers Island]; Male syntype from Aurora, West Virginia in USNM (Adamski gen. slide no. 2455).

ornatella Dietz, 1900a: 107, pl. VI, fig. 7, **Pigritia;** SYNTYPES (7 females, 1 male), MCZ 2929; Adamski gen. slide nos. 2182, 2183, 2184, 2186, 2187 females, 2185 male; 2 syntypes not dissected; United States: Pennsylvania, Hazleton; 1 specimen erroneously labeled as "*ornatella*" in USNM (Adamski gen. slide no. 2480 — female); 1 erroneously sexed syntype in MCZ.

pallidotinctella Dietz, 1900a: 111, pl. VII, fig. 8, 8a (male), 8b (female), **Epigritia;** SYNTYPES (2 of 3), MCZ 2915; both specimens missing abdomens; United States: Pennsylvania, Hazleton; *Epigritia ochromella* (Clemens); Male erroneously labeled as cotype in USNM (Adamski gen. slide no. 2482); 1 syntype lost.

plagiatella Dietz, 1910: 40, pl. III, fig. 20, **Holcocera;** HOLOTYPE male, MCZ 2957; Adamski gen. slide no. 2124; United States: Arizona, [Williams].

plummerella Dietz, 1910: 8, pl. I, fig. 4, **Blastobasis;** SYNTYPES (2 males of 6), MCZ 2961; Adamski gen. slide no. 2043 (one specimen missing abdomen); United States: Maryland, Plummer's [sic] Island; 3 syntypes in USNM (not dissected); 1 syntype lost.

pulchella Dietz, 1910: 20, pl. II, figs. 12, 12a, **Euresia;** HOLOTYPE male, MCZ 2967; Adamski gen. slide no. 2058; United States: District of Columbia, Washington.

purpurella Dietz, 1900a: 105, **Pigritia;** SYNTYPES (3 of 3 females), MCZ 2926; Adamski gen. slide nos. 2188, 2189, 2190; United States: Pennsylvania, Hazleton.

pusilla Dietz, 1910: 65, pl. IV, fig. 37, **Holcocera;** HOLOTYPE male, MCZ 2935; Adamski gen. slide no. 2139; United States: Texas, Brownsville.

quaintancella Dietz, 1910: 15, pl. I, fig. 9, **Valentinia;** SYNTYPES (2 females of 6), MCZ 2965; Adamski gen. slide nos. 2055, 2056; United States: locality unknown, bred from apple, Quaintance; 4 syntypes in USNM; 1 dissected (Adamski gen. slide no. 2416 — female), 2 missing abdomens, 1 with broken ovipositor.

quisquiliella Zeller, 1873: 298, **Blastobasis;** SYNTYPES (3 of 5), MCZ 1712, 1 male and 2 females; Adamski gen. slide nos. 2072, 2073; United States: Texas, [Dallas], Boll; *Holcocera chalcofrontella quisquiliella* (Zeller); 1 female is missing abdomen.

reductella Dietz, 1910: 45, **Holcocera funebra** var.; SYNTYPES (1 of 2), MCZ 2959, Adamski gen. slide no. 2095 (male); Canada: Manitoba, Aweme, Criddle; 1 syntype in USNM (missing abdomen).

rufopunctella Dietz, 1910: 65, **Holcocera;** HOLOTYPE female, MCZ 2936; Adamski gen. slide no. 2140; United States: Colorado, Denver, Oslar.

sagitella Dietz, 1910: 9, pl. I, fig. 5, **Blastobasis;** HOLOTYPE male, MCZ 2964; Adamski gen. slide no. 2046; United States: Pennsylvania, Hazleton [Aug. 2, 1898].

sciaphilella Zeller, 1873: 295, fig. 34, **Blastobasis;** HOLOTYPE male, MCZ 1713; Adamski gen. slide no. 2141; United States: Texas, [Dallas], Boll; *Holcocera sciaphilella* (Zeller).

simplicella Dietz, 1910: 9, **Blastobasis plummerella** var.; HOLOTYPE male, MCZ 2963; Adamski gen. slide no. 2045; United States: Iowa, Iowa City; Specimen originally misidentified as female.

simulella Dietz, 1910: 52, pl. III, fig. 28, **Holcocera;** SYNTYPES (2 of 4), MCZ 2944, female; Adamski gen. slide no. 2143; 1 syntype missing abdomen. United States: Arizona, Williams; Texas, Fedora; 1 syntype from Williams, Arizona in USNM (Adamski gen. slide no. 2459 — female); syntype from Stockton, Utah lost.

spoliatella Dietz, 1900: 110, **Pigritia;** SYNTYPES (2 of 2 males), MCZ 2913; Adamski gen. slide nos. 2191, 2192; 1 syntype missing left forewing and abdomen; United States: Pennsylvania, Hazleton; An additional damaged MCZ specimen is probably not a syntype. 1 specimen erroneously labeled co-type in USNM.

spoliatella Dietz, 1910: 53, **Holcocera messelinella** var., SYNTYPES (3 of 6), MCZ 2946, 3 males; Adamski gen. slide nos. 2117, 2118, 2119; United States: Pennsylvania, Hazleton; *Holcocera messelinella* Dietz; 3 syntypes lost including those from New Jersey.

spretella Dietz, 1910: 58, pl. IV, fig. 32, **Holcocera;** SYNTYPE (1 of 4), MCZ 2931; Adamski gen. slide no. 2145 — female; United States: Arizona, Phoenix. 3 syntypes from Williams, Arizona in USNM (Adamski gen. slides nos. 2144 — female, 2460 — male).

subsenella Zeller, 1873: 302, **Hypatima punctiferella** var.; HOLOTYPE male, MCZ 1716; Adamski gen. slide no. 2126, United States: Texas, [Dallas], Boll; *Holcocera punctiferella subsenella* (Zeller); Missing left wings; right forewing in gelatin capsule.

tartarella Dietz, 1910: 64, pl. IV, fig. 36, **Holcocera;** SYNTYPES (3 of 9), MCZ 2934, 1 male, 1 female; Adamski gen. slide nos. 2146, 2147; 1 not dissected; United States, Maryland, Plummer's [sic] Island, A. Busck. 3 syntypes in USNM; 2 missing abdomens; 1 dissected (Adamski gen. slide no. 2461 — male); 3 syntypes lost.

tenebrella Dietz, 1900a: 116, **Dryope;** SYNTYPES (2 of 3), MCZ 14220, 1 male, Adamski gen. slide no. 2233; United States: Pennsylvania, Hazleton; *Dryoperia tenebrella* (Dietz); 1 syntype missing abdomen; 1 syntype lost.

triangularisella Chambers, 1875b: 256, **Holcocera;** SYNTYPE (1 male of 2) MCZ 1550; Adamski gen. slide no. 2142, United States: [Kentucky, Chambers]; *Holcocera sciaphilella* (Zeller).

tristella Dietz, 1900a: 108, **Pigritia;** SYNTYPES (2 of 2 females) MCZ 2911; Adamski gen. slide nos. 2193, 2194, United States: Pennsylvania, Hazleton; 1 specimen erroneously labeled as "type" (type no. 6132) in USNM.

vestaliella Dietz, 1910: 63, pl. IV, fig. 35, **Holcocera;** SYNTYPES (3 of 6), MCZ 2933, all missing abdomens. United States, Maryland, Plummer's [sic] Island, Pennsylvania, Hazleton; 2 male syntypes from Plummers Island, Maryland (R. B. Selander gen. slide no. 703 and Adamski gen. slide no. 2469) in USNM. 1 syntype from Cohasset, Massachusetts, lost.

yuccaecolella Dietz, 1900: 7, pl. 1, fig. 3, **Blastobasis;** SYNTYPES (2 of 5), MCZ 2979, male and female; Adamski gen. slide nos. 2047, 2048, United States: Texas, bred from *Yucca baccata*, emerged 18 April 1897; 3 syntypes in USNM (not dissected).

zelleriella Dietz, 1910: 62, pl. IV, fig. 34, **Holcocera;** SYNTYPES (2 of 2 males), MCZ 2081; Adamski gen. slide nos. 2148, 2149; United States: Texas, Dallas; Only 1 male has locality label.

Family Momphidae

alboeapitella Chambers, 1875d: 33, **Laverna;** SYNTYPE, MCZ 1374; United States: Texas, Basque [sic] County, September; *Mompha murtfeldtella* (Chambers).

bicristatella Chambers, 1880b: 187, **Elachista;** SYNTYPE, MCZ 1355; United States: Texas, Belfrage; *Mompha bicristatella* (Chambers).

cephalonthiella Chambers, 1871b: 221, **Laverna;** SYNTYPES (6), MCZ 1372; United States: Kentucky, Chambers; *Mompha cephalonthiella* (Chambers).

circumscriptella Zeller, 1873: 312, fig. 42, **Laverna;** PSEUDOTYPE, MCZ 1380; United States: Texas, Dallas, Boll; *Mompha circumscriptella* (Zeller).

coloradella Chambers, 1877d: 136, **Laverna(?);** SYNTYPE, MCZ 1379; United States: Colorado, Edgerton, July; *Mompha coloradella* (Chambers).

definitella Zeller, 1873: 111, fig. 41, **Laverna;** SYNTYPE, MCZ 1377; United States: Texas, Dallas, Boll; *Mompha definitella* (Zeller).

grisseella Chambers, 1875c: 295, **Laverna;** PSEUDOTYPES (2), MCZ 14970; *Mompha murtfeldtella* (Chambers); MCZ has 2 specimens from Kentucky, but description was based on 3 specimens from Spanish Bar, Colorado.

ignobilisella Chambers, 1875d: 33, 51, **Laverna;** SYNTYPE, MCZ 1519; United States: Texas, Basque [sic] County, September; *Mompha ignobilisella* (Chambers).

murtfeldtella Chambers, 1875b: 237, **Laverna;** HOLOTYPE, MCZ 1375; United States: [Missouri, 15 September 1874, Murtfeldt]; *Mompha murtfeldtella* (Chambers).

obscurusella Chambers, 1875d: 53, **Laverna;** HOLOTYPE, MCZ 1371; United States: Texas, Basque [sic] County; *Mompha murtfeldtella* (Chambers).

oenotheraesemenella Chambers, 1876b: 138, **Laverna;** SYNTYPE, MCZ 14969; United States: Missouri; *Mompha brevivittella* (Clemens).

tricristatella Chambers, 1875e: 211, **Leucophryne;** SYNTYPE, MCZ 1381; Canada; *Mompha tricristatella* (Chambers).

unifasciella Chambers, 1876b: 159, **Laverna;** SYNTYPE, MCZ 1378; United States: California; *Mom-*

pha unifasciella (Chambers); Missing hindwings and abdomen.

Family Agonoxenidae

bicristatella Chambers, 1875e: 210, **Gelechia;** SYNTYPES (2), MCZ 1459; Canada; *Blastodacna bicristatella* (Chambers).

bipunctella Chambers, 1880: 187, **Aetia;** SYNTYPE, MCZ 1360; United States: Texas.

Family Cosmopterigidae

albalineella Chambers, 1878c: 95, **Eriphia?;** HOLOTYPE female, MCZ 14965; United States: Texas, Bosque County; *Eralea albalineella* (Chambers).

concolorella Chambers, 1875d: 55, **Elachista?;** HOLOTYPE female, MCZ 1352; United States: Texas, Bosque County; *Periploca orichalcella* (Clemens).

concolorella Chambers, 1875d: 55, **Eriphia;** LECTOTYPE male, MCZ 1356; United States: Texas; *Ithome concolorella* (Chambers); Lectotype designated by Hodges (1961b: 87), also 3 paralectotypes in MCZ.

determinatella Zeller, 1873: 289, **Oecophora;** HOLOTYPE male, MCZ 1710; United States: Texas; *Triclonella determinatella* (Zeller).

erransella Chambers, 1874a: 52, **Perimede;** HOLOTYPE, MCZ 1521; United States: Kentucky, Covington, Chambers; Description based on one specimen, but 4 specimens present in MCZ.

gleditschiaeella Chambers, 1876b: 135, **Laverna(?) (Anybia?);** LECTOTYPE male, MCZ 1373; United States: Kentucky, Chambers; *Periploca gleditschiaeella* (Chambers); Lectotype designated by Hodges (1962a: 88), also paralectotype in MCZ.

misecolorella Chambers, 1875d: 51, **Laverna;** LECTOTYPE male, MCZ 1370; United States: Texas, Bosque County; *Walshia miscecolorella* (Chambers); Lectotype designated by Hodges (1961a: 70).

montisella Chambers, 1875c: 297, **Cosmopteryx** [sic]; HOLOTYPE, MCZ 14967; United States: Colorado, Spanish Bar; *Cosmopterix montisella* Chambers.

nigrilineella Chambers, 1878c: 96, **Eriphia?;** HOLOTYPE male, MCZ 1357; United States: Texas, Bosque County; *Melanocinclis nigrilineella* (Chambers).

ostryaeella Chambers, 1874a: 74, **Aeaea;** HOLOTYPE male, MCZ 14966; United States: Kentucky; *Stilbosis ostryaeella* (Chambers).

purpuriella Chambers, 1874a: 73, **Chrysopeleia;** SYNTYPES (3), MCZ 1358; United States: Kentucky.

quadricustatella Chambers, 1880b: 186, **Aeaea;** HOLOTYPE male, MCZ 1359; United States: Texas, Waco; *Stilbosis quadricustatella* (Chambers).

4-lineella Chambers, 1878c: 95, **Cosmopteryx** [sic]; HOLOTYPE female, MCZ 1518; United States: Texas, Bosque County; *Cosmopterix quadrilineella* Chambers.

sexnotella Chambers, 1878c: 88, **Gelechia;** HOLOTYPE, MCZ 1542; United States: Texas, Bosque County; *Stagmatophora sexnotella* (Chambers).

unimaculella Chambers, 1875d: 94, **Ithome;** LECTOTYPE male, MCZ 1520; United States: Texas; *Ithome concolorella* (Chambers); Lectotype designated by Hodges (1961b: 87), and paralectotype in MCZ.

Family Scythrididae

albapenella Chambers, 1875d: 11, **Butalis;** SYNTYPE male, MCZ 1516; United States: Texas, Basque [sic] County, October; "*Scythris*" *albapenella* (Chambers) [misplaced]; Specimen in poor condition, missing left wings, and part of thorax.

arizoniella Kearfott, 1907: 8, **Holcocera;** SYNTYPE, MCZ 15022; United States: Arizona, Phoenix, October, Kunze; *Scythris eburnea* (Walsingham).

immaculatella Chambers, 1875d: 10, **Butalis;** SYNTYPE, MCZ 1515; United States: Texas, Basque [sic] County, April; *Scythris impositella* (Zeller).

plausipennella Chambers, 1875d: 10, **Butalis;** SYNTYPE, MCZ 1517; United States: Texas, Basque [sic] County; *Scythris plausipennella* (Chambers); Missing left wings.

Family Gelechiidae

albimarginella Chambers, 1875c: 291, **Gelechia;** SYNTYPE male, MCZ 2992; United States: Colorado, Grand River; *Gnorimoschema albimarginella* (Chambers); Abdomen and left wings missing. Specimen (MCZ 2992) probably is incorrectly labelled Kentucky. It matches a specimen from West Fork of Oak Creek, Coconino County, Arizona; and the type locality is Grand River, Colorado.

albistrigella Chambers, 1872a: 171, **Gelechia;** "SYNTYPES" (2), MCZ 1522; United States: Kentucky, June, Chambers; *Untomia albistrigella* (Chambers); *Untomia albistrigella* was described from a single specimen; one of the specimens is a false type.

amorphaeella Chambers, 1877a: 124, **Gelechia;** SYNTYPES (3 of 4), MCZ 1480; United States: Colorado, Edgerton, Chambers; *Filatima ornatifimbriella* (Clemens).

anarsiella Chambers, 1877a: 126, **Gelechia;** SYNTYPES (8), MCZ 1484; United States: Colorado, Edgerton, Chambers.

apicistrigella Chambers, 1872a: 66, **Parasia:** HOLOTYPE female, MCZ 1523; United States: Kentucky, Chambers; *Battaristis nigratomella* (Clemens). Specimen lacks abdomen and right hindwing.

atrupictella Dietz, 1900: 350, **Eucordylea;** HOLOTYPE male, MCZ 2986; United States: Pennsylvania, Hazleton; *Coleotechnites atrupictella* (Dietz).

basifasciella Zeller, 1873: 269, **Gelechia (Poecilia?);** HOLOTYPE male, MCZ 2988; United States: Texas, Boll; *Pseudotelphusa basifasciella* (Zeller).

basistrigella Zeller, 1873: 270, **Gelechia;** HOLOTYPE female, MCZ 2981; United States: Texas, Boll; *Xenolechia basistrigella* (Zeller).

bifasciella Chambers, 1874a: 76, **Gelechia;** SYNTYPE male, MCZ 1362; United States: Kentucky, Chambers; *Theisoa constrictella* (Zeller).

bifidella Dietz, 1900: 351, **Nealyda;** SYNTYPE male, MCZ 2990; United States: Colorado, Glenwood Springs.

bimaculella Chambers, 1877d: 122, **Nothris?;** HOLOTYPE male, MCZ 1557; United States: Colorado, Edgerton; *Dichomeris georgiella* (Walker).

bimaculella Chambers, 1872a: 108, **Depressaria;** SYNTYPE female, MCZ 1524; United States: Kentucky, Chambers; *Fascista bimaculella* (Chambers).

biminimaculella Chambers, 1880b: 183, **Gelechia;** SYNTYPES (2), MCZ 1525; United States: Texas, Waco, Belfrage; *Filatima biminimaculella* (Chambers).

bicolorella Chambers, 1872a: 195, **Agnippe;** SYNTYPE female, MCZ 1281; United States: Kentucky, Chambers.

bosquella Chambers, 1875d: 92, **Oecophora;** SYNTYPE female, MCZ 1443; United States: Texas; *Stegasta bosquella* (Chambers); Right hindwing missing.

canopulvella Chambers, 1878c: 91, **Gelechia;** HOLOTYPE female, MCZ 1152; United States: Texas, Bosque County; *Filatima obscurosuffusella* (Chambers).

cercerisella Chambers, 1872a: 108, **Depressaria;** SYNTYPES (2), MCZ 1427; United States: Kentucky, Chambers; *Fascista cercerisella* (Chambers); Specimens are double mounted on one block of pith. Male lacks head, female lacks left forewing and abdomen.

cihalinella Chambers, 1874b: 242, **Gelechia;** SYN-[illegible] United States: Texas, *Isophrictis* [illegible]

collinusella Chambers, 1877d: 128, **Gelechia;** HOLOTYPE male, MCZ 1526; United States: Colorado, Edgerton; *Gnorimoschema collinusella* (Chambers); Right wings only.

concinnusella Chambers, 1875b: 253, **Gelechia;** SYNTYPES (2), MCZ 1460; United States: Texas; *Battaristis concinnusella* (Chambers).

consonella Zeller, 1873: 251, **Gelechia;** SYNTYPE male, MCZ 2982; United States: Texas, Boll; *Anacampsis rhoifructella* (Clemens).

costarufoella Chambers, 1874b: 240, **Gelechia;** LECTOTYPE, MCZ 1527; United States: Texas, Chambers; *Dichomeris costarufoella* (Chambers); Lectotype designated by Hodges (1986: 114).

crescentifasciella Chambers, 1874b: 237, **Gelechia;** SYNTYPES (7), MCZ 1477; United States: Texas; *Compsolechia crescentifasciella* (Chambers).

cristatella Chambers, 1875b: 241, **Gelechia;** SYNTYPES (2), MCZ 1472; United States: Kentucky, Chambers; *Coleotechnites cristatella* (Chambers).

cristifasciella Chambers, 1878c: 87, **Gelechia;** SYNTYPE female, MCZ 1474; United States: Kentucky, 11 May [no year stated], Chambers; *Arogalea cristifasciella* (Chambers); Worn specimen. Described from two syntypes.

curvistrigella Chambers, 1872a: 133, **Telphusa;** SYNTYPE female, MCZ 2939; United States: Kentucky, Chambers; *Telphusa longifasciella* (Clemens); Abdomen missing.

depressostrigella Chambers, 1874b: 236, **Gelechia;** SYNTYPES (2), MCZ 1434; United States: Texas; *Filatima ochreosuffusella* (Chambers).

disconotella Chambers, 1878c: 86, **Gelechia;** SYNTYPE, MCZ 1475; United States: Kentucky, Chambers; *Monochroa disconotella* (Chambers); Left wings missing.

discoocellella Chambers, 1872a: 194, **Gelechia;** SYNTYPES (4), MCZ 1439; United States: Kentucky, September, Chambers; *Chionodes discoocellella* (Chambers).

dorsivittella Zeller, 1873: 265, fig. 20, **Gelechia (Teleia?);** HOLOTYPE male, MCZ 1707; United States: Texas, Dallas, Boll; *Coleotechnites vagatioella* (Chambers); Haustellum and abdomen missing.

dubitella Chambers, 1872a: 92, **Depressaria?;** LECTOTYPE male, MCZ 1529; United States: Kentucky, Chambers; *Dichomeris juncidella* (Clemens); Lectotype designated by Hodges (1986: 111).

elegantella Chambers, 1874b: 239, **Gelechia;** SYNTYPES (8), MCZ 1494; United States: Texas, Chambers; *Aristotelia elegantella* (Chambers).

eupatoriella Chambers, 1872a: 221, **Ypsolophus;** LECTOTYPE male, MCZ 1531; United States: [Kentucky], Chambers; *Dichomeris setosella* (Cle-

mens); The original description indicates that one specimen was reared; it should be the holotype. None of the specimens bearing MCZ 1531 could be recognized as the one that Chambers described. Hodges (1986: 82) designated one of the four as lectotype.

fragmentella Zeller, 1873: 271, **Gelechia (Poecilia?);** HOLOTYPE female, MCZ 1706; United States: Texas, Dallas, Boll; *Pseudotelphusa quercinigracella* (Chambers); Specimen lacks right wings and abdomen.

fuscocristatella Chambers, 1875d: 9, **Naera;** SYNTYPES (4), MCZ 1382; United States: Texas.

fuscoluteella Chambers, 1872a: 106, **Depressaria;** HOLOTYPE male, MCZ 1462; United States: Kentucky, Chambers; *Gelechia albisparsella* (Chambers); Abdomen missing.

fuscomaculella Chambers, 1872a: 170, **Gelechia;** HOLOTYPE male, MCZ 1469; United States: Kentucky, Chambers; *Chionodes fuscomaculella* (Chambers).

fuscoochrella Chambers, 1872a: 106, **Gelechia;** SYNTYPE female, MCZ 1532; United States: Kentucky, Chambers; *Chionodes mediofuscella* (Clemens).

fuscopalidella Chambers, 1875b: 231, **Sinoe;** SYNTYPES (3), MCZ 1533; United States: Kentucky, Chambers; *Sinoe robiniella* (Fitch); One specimen has the left forewing; the other specimen has the right forewing.

fuscopulvella Chambers, 1872a: 195, **Agnippe;** HOLOTYPE male, MCZ 1282; United States: Kentucky, April, Chambers.

fuscopulvella Chambers, 1872a: 170, **Gelechia;** HOLOTYPE female, MCZ 1492; United States: Kentucky, June, Chambers; *Chionodes obscurusella* (Chambers).

fuscostrigella Chambers, 1876b: 30, **Polyhymno;** HOLOTYPE male, MCZ 1547; United States: Texas, Belfrage; *Polyhymno luteostrigella* Chambers; Abdomen missing; labial palpus nearly devoid of scales ventrally.

fuscotaeniaella Chambers, 1878c: 89, **Gelechia;** HOLOTYPE male, MCZ 1448; United States: Texas; *Rifseria fuscotaeniaella* (Chambers); Head, thorax, and left wings only.

gilviscopella Zeller, 1873: 266, **Gelechia;** SYNTYPES (2), MCZ 1708; United States: Texas, Dallas, Boll; *Coleotechnites quercivorella* (Chambers).

glandiferella Zeller, 1873: 275, **Gelechia;** PARALECTOTYPE female, MCZ 1709; United States: Texas; *Deltophora glandiferella* (Zeller); Lectotype in BMNH designated by Sattler (1979: 297).

glycyrhizaeella Chambers, 1877a: 124, **Gelechia;** HOLOTYPE female, MCZ 1483; United States: Colorado, Edgerton; *Filatima glycyrhizaeella* (Chambers); Abdomen missing.

innocuella Zeller, 1873: 249, **Gelechia (Tachyptilia);** SYNTYPE male, MCZ 1721; United States: Texas, Boll; *Anacampsis innocuella* (Zeller).

intermediella Chambers, 1879a: 89, **Gelechia;** HOLOTYPE female, MCZ 1447; United States: Texas, Bosque County; *Aristotelia intermediella* (Chambers); Labial palpi, metathorax, and abdomen missing.

inversella Zeller, 1873: 248, **Epicorthylis;** HOLOTYPE male, MCZ 1715; United States: Texas, Boll; *Dichomeris inversella* (Zeller).

latifasciella Chambers, 1875b: 251, **Gelechia;** PSEUDOTYPE female, MCZ 2940; United States: Missouri, St. Louis; *Telphusa latifasciella* (Chambers); The original description indicates that the moth is light. The specimen (MCZ 2940) is dark and represents the dark form of *latifasciella*.

lavernella Chambers, 1874b: 242, **Gelechia;** HOLOTYPE female, MCZ 1473; United States: Texas; *Symmetrischema lavernella* (Chambers).

leuconota Zeller, 1873: 268, **Gelechia;** HOLOTYPE male, MCZ 2973; United States: Texas, Boll; *Evippe leuconota* (Zeller).

liturosella Zeller, 1873: 265, **Gelechia (Lita);** HOLOTYPE female, MCZ 1704; United States: Texas, Dallas, Boll; *Chionodes mediofuscella* (Clemens).

luteostrigella Chambers, 1874b: 247, **Polyhymno;** PSEUDOTYPE female, MCZ 1546; United States: Texas; The specimen (MCZ 1546) is a *Coleophora*. The original description applies to the current concept of the gelechiid species *Polyhymno luteostrigella*.

maculimarginella Chambers, 1874b: 241, **Gelechia;** SYNTYPES (2), MCZ 1446; United States: Texas; *Chionodes fuscomaculella* (Chambers).

marmorella Chambers, 1875b: 239, **Gelechia;** HOLOTYPE, MCZ 1471; United States: Kentucky, Chambers; *Gnorimoschema emancipatum* (Meyrick), REVISED STATUS; *Gelechia marmorella* Chambers, 1875 is a junior primary homonym of *Gelechia marmorella* Doubleday, 1859. *Phthorimaea emancipata* Meyrick, 1925 is an objective replacement name for *Gelechia marmorella* Chambers, 1875.

minimaculella Chambers, 1874b: 235, **Gelechia;** HOLOTYPE male, MCZ 1485; United States: Texas; *Aroga thoracealbella* (Chambers).

minimella Chambers, 1874b: 243, **Gelechia;** SYNTYPES (2), MCZ 1487; United States: Texas; *Aristotelia pullusella* (Chambers).

monumentella Chambers, 1877d: 125, **Gelechia;** HOLOTYPE male, MCZ 1482; United States: Colo-

rado, Monument Park; *Scrobipalpa monumentella* (Chambers).

multifasciella Chambers, 1875d: 93, **Theisoa;** SYNTYPE, MCZ 1363; United States: Texas.

nigrella Chambers, 1875b: 250, **Gelechia;** PSEUDOTYPE, MCZ 1489; United States: Texas; *Syncopacma nigrella* (Chambers); The single, abdomenless specimen does not match the original description.

nonstrigella Chambers, 1878c: 92, **Dasycera;** HOLOTYPE male, MCZ 1544; United States: Kentucky, Chambers; *Dichomeris nonstrigella* (Chambers).

obliquifasciella Chambers, 1880b: 182, **Gelechia;** HOLOTYPE male, MCZ 1470; United States: Texas; *Telphusa longifasciella* (Clemens).

obliquistrigella Chambers, 1872a: 65, **Anarsia;** SYNTYPES (2), MCZ 1535; United States: Kentucky, Chambers; *Coleotechnites obliquistrigella* (Chambers).

obscurosuffusella Chambers, 1878c: 90, **Gelechia;** SYNTYPE female MCZ 1453; United States: Texas, Bosque County; *Filatima obscurosuffusella* (Chambers); Abdomen and left forewing missing.

obscurusella Chambers, 1872a: 106, **Depressaria;** SYNTYPE male, MCZ 1632; United States: Kentucky, Chambers; *Chionodes obscurusella* (Chambers).

occidentella Chambers, 1875b: 246, **Gelechia;** SYNTYPE female, MCZ 1464; United States: California, Behrens; *Chionodes occidentella* (Chambers).

ocellella Chambers, 1877a: 126, **Gelechia?;** HOLOTYPE male, MCZ 1440; United States: Colorado, Edgerton; *Gelechia bianulella* (Chambers); The holotype is a male, not a female as indicated by Chambers.

ochreocostella Chambers, 1878c: 91, **Gelechia;** HOLOTYPE female, MCZ 1455; United States: Texas, Bosque County; *Anacampsis rhoifructella* (Clemens).

ochreostrigella Chambers, 1875b: 247, **Gelechia;** HOLOTYPE male, MCZ 1463; United States: California, Behrens; *Chionodes ochreostrigella* (Chambers). Abdomen missing.

ochreostrigella Chambers, 1877a: 126, **Gelechia;** SYNTYPES (3), MCZ 2995; United States: Colorado, Edgerton; *Scrobipalpula henshawiella* (Busck); The syntypes represent two species.

olympiadella Zeller, 1873: 259, **Gelechia;** PSEUDOTYPES 2 males, MCZ 2921; United States: Texas; *La[illegible] cercerisella* (Chambers); These specimens were not seen by Zeller when he described [illegible].

pallidastrigella Chambers, 1874b: 244, **Cleodora;** SYNTYPE, MCZ 1561; United States: Texas; *Isophrictis pallidastrigella* (Chambers).

pallidella Chambers, 1874b: 245, **Cleodora;** SYNTYPES (2), MCZ 1562; United States: Texas; *Isophrictis pallidella* (Chambers); The specimens are very poor and probably represent two species.

pallidochrella Chambers, 1872a: 126, **Depressaria;**; HOLOTYPE female, MCZ 1536; United States: Kentucky, May, Chambers; *Symmetrischema pallidochrella* (Chambers).

pallidochrella Chambers, 1873a: 188, **Helice;** SYNTYPES (4), MCZ 1620; (13), MCZ 1534; United States: Kentucky, Chambers; *Theisoa pallidochrella* (Chambers); Two MCZ type numbers with associated specimens represent the same species.

palpiannulella Chambers, 1872a: 68, **Gelechia;** SYNTYPES (4), MCZ 1493; United States: Kentucky, Chambers; *Monochroa absconditella* (Walker).

palpilineella Chambers, 1875b: 252, **Gelechia;** SYNTYPES (3), MCZ 1486; United States: Kentucky, Chambers; *Syncopacma palpilineella* (Chambers).

pedmontella Chambers, 1877a: 123, **Gelechia;** HOLOTYPE male, MCZ 1478; United States: Colorado, Edgerton; *Gnorimoschema pedmontella* (Chambers).

pennsylvanica Dietz, 1900b: 353, **Pseudochelaria;** HOLOTYPE female, MCZ 2974; United States: Pennsylvania, Hazleton.

physaliella Chambers, 1872a: 173, **Gelechia;** SYNTYPE female, MCZ 33255; United States: Kentucky, Chambers; *Aristotelia physaliella* (Chambers); Chambers described *physaliella* from two specimens reared from *Physalis viscosa* L. The specimen in the MCZ was received from the Peabody Academy collection. A second syntype is in USNM.

platanella Chambers, 1872a: 146, **Cirrha;** PSEUDOTYPE male, MCZ 1430; United States: Kentucky, Chambers; *Gelechia albisparsella* (Chambers); *Cirrha platanella* Chambers is a replacement name for *Depressaria albisparsella* Chambers and as such does not have a separate type from the name it replaces. However, no type material of *albisparsella* exists. This specimen could be considered for designation as neotype of *albisparsella*. It has only the head, thorax, and right forewing.

plutella Chambers, 1874b: 238, **Gelechia;** PSEUDOTYPES (2), MCZ 1429; United States: Kentucky; *Dichomeris serrativittella* (Zeller); These specimens are from Kentucky, not Texas as stated in the original description, and the color pattern on the forewings is reversed from that of the original description.

plutella Chambers, 1874b: 244, **Neda;** SYNTYPES (2), MCZ 1369; United States: Texas; *Megacraspedus plutella* (Chambers); Another syntype in USNM.

plutella Chambers, 1875d: 106, **Phaetusa;** PSEUDOTYPES (2), MCZ 1429; United States: Kentucky; *Evippe leuconota* (Zeller); These specimens are from Kentucky, not Texas as stated in the original description. One female syntype in USNM.

prunifoliella Chambers, 1873a: 186, **Evippe;** SYNTYPE male, MCZ 1537; United States: Kentucky, Chambers.

pseudacaciella Chambers, 1872a: 107, **Depressaria;** SYNTYPES (11), MCZ 1490; United States: Kentucky, Chambers; *Filatima pseudacaciella* (Chambers).

pudibundella Zeller, 1873: 273, **Aristotelia;** LECTOTYPE male, MCZ 1441; United States: Texas, Dallas, Boll; Lectotype designated by Forbes (1932: 429).

quadrimaculella Chambers, 1874b: 237, **Gelechia;** LECTOTYPE male, MCZ 1436; United States: Texas; *Anacampsis rhoifructella* (Clemens); The lectotype, present designation, bears the following labels: 1)"Type 1436"; 2)"*Gelechia quadrimaculella* Cham. Texas"; 3)"*Anacampsis rhoifructella* Clem. =*quadrimaculella* Cham. AB 1902"; 4)"Lectotype R. W. Hodges. It is selected to ensure that the name continues to be associated with *Anacampsis rhoifructella* (Clemens). The second syntype is a species of *Neodactylota*.

querciella Chambers, 1872a: 127, **Depressaria;** SYNTYPES (3), MCZ 1538; United States: Kentucky, Chambers; *Neotelphusa querciella* (Chambers).

querciella Chambers, 1872a: 223, **Ypsolophus;** PSEUDOTYPE female, MCZ 1560; United States: Kentucky, Chambers; *Dichomeris ventrella* (Fitch); The identification label reads "*Ypsolophus quercicoella* var. *pomatella* 482/1", and the specimen is *Dichomeris ligulella* Huebner. The original description of *querciella* clearly states that the wings are broad and thus does not apply to this specimen.

quercinigracella Chambers, 1872a: 170, **Gelechia;** HOLOTYPE male, MCZ 1701; United States: Kentucky, Chambers; *Pseudotelphusa quercinigracella* (Chambers); Abdomen and right wings missing.

quercipominella Chambers, 1872a: 222, **Ypsolophus;** HOLOTYPE female, MCZ 1560; United States: Kentucky, Chambers; *Dichomeris ligulella* Huebner.

quercivorella Chambers, 1872a: 173, **Gelechia;** HOLOTYPE female, MCZ 1539; United States: Kentucky, Chambers; *Coleotechnites quercivorella* (Chambers).

quinqueannulella Chambers, 1872a: 191, **Gelechia;** HOLOTYPE female, MCZ 1467; United States: Kentucky, Chambers; *Trypanisma prudens* Clemens.

reedella Chambers, 1872a: 222, **Ypsolophus;** SYNTYPES (3), MCZ 1559; United States: Kentucky, Chambers; *Dichomeris ligulella* Huebner; The three specimens are the same species.

ribesella Chambers, 1875c: 290, **Gelechia;** HOLOTYPE female, MCZ 2984; United States: Colorado, Spanish Bar, Clear Creek.

rileyella Chambers, 1872a: 106, **Depressaria;** SYNTYPE male, MCZ 1431; United States: Kentucky, Chambers; *Gelechia rileyella* (Chambers).

rubensella Chambers, 1872a: 193, **Gelechia;** PSEUDOTYPES (3), MCZ 1449; United States: Kentucky, Chambers; *Aristotelia rubidella* (Clemens); The status of these specimens as types is questionable. Chambers described *rubensella* from a single specimen that had its fringes singed by a gas light. None of these is singed.

rufusella Chambers, 1874b: 240, **Gelechia;** SYNTYPES (3), MCZ 1444; United States: Texas; *Anacampsis fullonella* (Zeller).

saphirinella Chambers, 1875b: 250, **Gelechia;** HOLOTYPE, MCZ 1468; United States: [Kentucky, Chambers]; *Gnorimoschema saphirinella* (Chambers); Labial palpi, right hindwing, and abdomen missing. The right forewing is glued on a block. Although the original description implies Texas as the type locality, the label states "Kentucky, Chambers."

saundersella Chambers, 1876b: 173, **Gelechia;** SYNTYPES (2), MCZ 1540; United States: Kentucky, Chambers; *Taygete saundersella* (Chambers).

scutellariaeela Chambers, 1873a: 175, **Gelechia;** SYNTYPE male, MCZ 1541; United States: Kentucky, Boone County, Verona; *Scrobipalpa scutellariaeela* (Chambers).

sella Chambers, 1874b: 238, **Gelechia;** LECTOTYPE male, MCZ 1481; United States: Texas; *Deltophora sella* (Chambers); Lectotype designated by Sattler (1979: 294).

serratipalpella Chambers, 1877a: 123, **Gelechia;** HOLOTYPE male, MCZ 1479; United States: Colorado, Edgerton; *Gnorimoschema serratipalpella* (Chambers); The abdomen is glued to the rest of the specimen.

serrativittella Zeller, 1873: 280, **Gelechia;** PARALECTOTYPE female, MCZ 1705; United States: Texas, Dallas, Boll; *Dichomeris serrativittella* (Zeller); Lectotype female in BMNH designated by Hodges (1986: 101).

sexstrigella Chambers, 1874b: 248, **Polyhymno?**: SYNTYPES (3), MCZ 1545; United States: Texas; *Calliprora sexstrigella* (Chambers).

solaniiella Chambers, 1873a: 176, **Gelechia**; PSEUDOTYPE female, MCZ 2453; *Isophrictis similiella* (Chambers); *Gelechia solaniiella* Chambers is a replacement name for *Gelechia similiella* Chambers, 1872.

straminiella Chambers, 1872a: 224, **Ypsolophus**; LECTOTYPE female, MCZ 1558; United States: Kentucky, Chambers; *Dichomeris punctidiscella* (Clemens); Lectotype designated by Hodges (1986: 54).

ternariella Zeller, 1873: 264, **Gelechia** (Lita); HOLOTYPE female, MCZ 1702; United States: Texas, Boll; *Fascista bimaculella* (Chambers).

texanella Chambers, 1880b: 179, **Anesychia**; LECTOTYPE male, MCZ 1424; United States: Texas; *Lita texanella* (Chambers); Lectotype designated by Hodges (1966: 30).

thoracealbella Chambers, 1874b: 235, **Gelechia**; SYNTYPE male, MCZ 1435; United States: Texas, Waco, Belfrage; *Aroga thoracealbella* (Chambers).

trialbamaculella Chambers, 1875b: 250, **Gelechia**; HOLOTYPE female, MCZ 1456; United States, Texas, Waco, Belfrage; *Aroga trialbamaculella* (Chambers); Head and right wings missing.

trifasciella Chambers, 1875b: 252, **Gelechia**; SYNTYPES (2), MCZ 1445; United States: Texas, Waco, Belfrage; *Filatima albilorella* (Zeller).

trilineella Chambers, 1877a: 125, **Gelechia**; SYNTYPES (6), MCZ 1454; United States: Colorado, Edgerton; *Aroga trilineella* (Chambers); One syntype is not conspecific with the other five.

trimaculella Chambers, 1874b: 243, **Anarsia**; LECTOTYPE male, MCZ 1556; United States: Texas, Waco, Belfrage; *Isophrictis trimaculella* (Chambers). The lectotype, present designation, bears the following labels: 1)"Type 1556"; 2)"Texas"; 3)"72"; 4)"996"; 5)"*trimaculella*"; 6)"Lectotype R W Hodges"; 7)"RWH genitalia slide 3314." It is selected to ensure continued use of the name in *Isophrictis*. Three species are represented among the syntypes.

trimaculella Chambers, 1874b: 238, **Gelechia**; PARALECTOTYPES (3), MCZ 1476; United States: Texas, Waco, Belfrage; *Helcystogramma melanocarpum* (Meyrick); Lectotype in USNM designated by Hodges (1986: 130).

trimaculella Packard, 1867: 61, **Gelechia**; SYNTYPES (2), MCZ 1563; Canada: Labrador, Strawberry Harbor; *Chionodes continuella* (Zeller).

triocellella Chambers, 1877a: 127, **Gelechia**; SYNTYPES (6), MCZ 1453; United States: Colorado, Edgerton; *Gnorimoschema triocellella* (Chambers).

unctulella Zeller, 1873: 257, **Gelechia**; HOLOTYPE male, MCZ 1703; United States: Texas, Boll; *Filatima ornatifimbriella* (Clemens).

variella Chambers, 1872a: 174, **Gelechia**; SYNTYPES (2 of several), MCZ 1544; United States: Kentucky, Chambers; *Coleotechnites variella* (Chambers); One female syntype is in USNM.

versutella Zeller, 1873: 253, **Gelechia**; HOLOTYPE female, MCZ 1457; United States: Texas, Boll.

violaceofusca Zeller, 1873: 258, **Gelechia**; HOLOTYPE male, MCZ 2981; United States: Texas, Dallas, Boll; *Chionodes discoocellella* (Chambers).

walsinghami Dietz, 1900b: 352, **Pseudochelaria**; SYNTYPE male, MCZ 3266; United States: Pennsylvania, Hazleton.

SUPERFAMILY COPROMORPHOIDEA

Family Glyphipterigidae

exoptatella Chambers, 1875b: 234, **Glyphipteryx** [sic]; HOLOTYPE, MCZ 1564; United States: Kentucky, Linden Grove Cemetery, [June], Chambers; *Diploschizia impigritella* (Clemens); Heppner (1981: 322) gives type locality as "[Covington?, Kenton Co.]."

montisella Chambers, 1875c: 292, **Glyphipteryx** [sic]; LECTOTYPE male, MCZ 32887; United States: Colorado, Denver, South Park, 10,000 feet; *Glyphipterix montisella* Chambers; Lectotype designated by Heppner (1985: 124).

SUPERFAMILY YPONOMEUTOIDEA

Family Plutellidae

NOTE: The Walsingham syntypes in this family were sent to Chambers by Walsingham. We suggest that lectotypes should be selected from syntypes at the BMNH because Walsingham's personal collection is there. He most likely sent syntypes (a term not used in the 1880s) to Chambers as examples of his species. Types (holotypes and lectotypes in current terms) he would have retained.

canariella Walsingham, 1881: 309, pl. XXXV, fig. 11, **Cerostoma**; SYNTYPES (2), MCZ 14982; United States: California, Lake County, Scott's Valley, 18 May 1871; *Ypsolopha canariella* (Walsingham).

castella Walsingham, 1881: 310, pl. XXXV, fig. 13, **Euceratia**; SYNTYPES (2), MCZ 14984; United States: California, San Francisco.

dentiferella Walsingham, 1881: 308, pl. XXXV, fig. 10, **Cerostoma;** SYNTYPES (2), MCZ 14985; United States: California, Mount Shasta, August 1871; *Ypsolopha dentiferella* (Walsingham).

falciferella Walsingham, 1881: 307, pl. XXXV, fig. 7, **Cerostoma;** SYNTYPE (1 of 18), MCZ 14988; United States: California and Oregon; *Ypsolopha falciferella* (Walsingham).

frustella Walsingham, 1881: 309, pl. XXXV, fig. 12, **Cerostoma;** SYNTYPES (2 of 26), MCZ 14981; United States: California, Shasta County, 28 July 1871; *Ypsolopha frustella* (Walsingham).

ochrella Chambers, 1880b: 181, **Pluteloptera;** SYNTYPE, MCZ 1414; United States: Texas, Belfrage; *Ypsolopha ustella* (Clemens); Missing left wings.

polita Walsingham, 1881: 302, pl. XXXV, fig. 2, **Calantica;** SYNTYPES (2), MCZ 14992; United States: California; *Eucalantica polita* (Walsingham).

securella Walsingham, 1881: 311, pl. XXXV, fig. 14, **Euceratia;** SYNTYPE (1 of 17), MCZ 14983; United States: California, Sonoma County, May 1871.

subfasciella Walsingham, 1881: 303, pl. XXXV, fig. 3, **Araeolepia;** PARALECTOTYPE (1 of 17), MCZ 14986; United States: Oregon, Currant Creek (an affluent of John Day River), 16 April 1872; Lectotype in BMNH designated by Heppner (1982: 278).

vanella Walsingham, 1881: 305, pl. XXXV, fig. 6, **Plutella;** SYNTYPE, MCZ 14987; United States: California, San Francisco.

Family Yponomeutidae

celastrusella Kearfott, 1903: 150, **Zelleria;** SYNTYPES (2), MCZ 14228; United States: New Jersey, Essex County, "Pk." and Caldwell.

crassivenella Zeller, 1872: 563, fig. 27, **Enaemia;** HOLOTYPE female, MCZ 15001; United States: Texas, Dallas, Boll; *Lactura pupula* (Huebner).

Family Argyresthiidae

altissimella Chambers, 1877d: 130, 147, **Argyresthia;** SYNTYPE, MCZ 1412; United States: Colorado, Mount Elbert, 11,000 feet, July.

austerella Zeller, 1873: 305, fig. 38, **Argyresthia;** SYNTYPES (3 of 6), MCZ 14254; United States: Texas, Dallas, Boll.

belangerella Chambers, 1875e: 145, **Argyresthia;** SYNTYPE, MCZ 1407; Canada; Missing right wings.

deletella Zeller, 1873: 305, **Argyresthia;** SYNTYPES (3), MCZ 14254; United States: Texas, Dallas, Boll.

montella Chambers, 1877d: 130, **Argyresthia;** SYNTYPE, MCZ 1411; United States: Colorado, Edgerton, July.

pedmontella Chambers, 1877d: 131, **Argyresthia;** SYNTYPES (2), MCZ 1409; United States: Colorado, Edgerton, July.

quadristrigella Zeller, 1873: 304, **Argyresthia;** HOLOTYPE male, MCZ 14252; United States: Texas, Dallas, Boll; Missing abdomen.

quercicolella Chambers, 1877d: 130, **Argyresthia;** SYNTYPES (2), MCZ 1410; United States: Colorado, Edgerton, June.

thuiella Packard, 1871: 24, pl. 1, fig. 6, **Bucculatrix;** SYNTYPES, MCZ 14963; United States: Maine, Brunswick, July, on cedar tree; *Argyresthia thuiella* (Packard); Fragments of several specimens in vial.

undulatella Chambers, 1874a: 10, **Argyresthia;** SYNTYPES (6), MCZ 1408; United States: Kentucky, Chambers.

Family Heliodinidae

abroniaeella Chambers, 1876b: 217, **Lithariapteryx;** SYNTYPES (9), MCZ 1565; United States: Colorado, Edgerton, over 6000 feet, July.

bella Chambers, 1875d: 73, **Aetole;** SYNTYPE, MCZ 1364; United States: Texas, August, Belfrage; *Heliodines bella* (Chambers).

SUPERFAMILY SESIOIDEA

Family Sesiidae

aureopurpura H. Edwards, 1880: 72, **Aegeria;**; HOLOTYPE female, MCZ 928; United States: Texas, Dallas, Boll; *Carmenta bassiformis* (Walker).

caudata Harris, 1839: 311, **Aegeria;**; SYNTYPES (1 male, 1 female), MCZ 26354; United States: [Massachusetts, Neponset River, 30 August 1823, Harris no. 87]; *Alcathoe caudata* (Harris).

cucurbitae Harris, 1828: 33, **Aegeria;**; SYNTYPES (5 adults and 5 pupal cases), MCZ 33258; United States: [Harris no. 249]; *Melittia cucurbitae* (Harris).

denudatum Harris, 1839: 310, **Trochilium;** SYNTYPE, MCZ 26359; United States: [Harris no. 311]; *Sesia asilipennis* (Boisduval).

fulvipes Harris, 1839: 312, **Aegeria;** SYNTYPE, MCZ 26361; United States: [Harris no. 17]; *Synanthedon fulvipes* (Harris).

maculipes Grote and Robinson, 1868, 184, **Zenodoxus;** PSEUDOTYPE female, MCZ 929; United States: Texas, Dallas, Boll; Not a syntype according to Duckworth and Eichlin (1978: 16).

marginatum Harris, 1839: 309, **Trochilium;** SYN-

TYPE female, MCZ 26356; United States: New Hampshire, [Dublin], L. W. Leonard [Harris no. 388]; *Pennisetia marginata* (Harris).

nebraskae H. Edwards, 1881: 181, **Euhagena:** HOLOTYPE male, MCZ 930, United States: Nebraska, Mr. Austin; Broken and in poor condition.

polistiformis Harris, 1854: 216, **Aegeria:** SYNTYPES (3 males, 2 females, 3 pupal cases), MCZ 26358; United States: North Carolina, Albermarle, F. J. Kron [Harris no. 791]; *Vitacca polistiformis* (Harris).

pyri Harris, 1830: 2, **Aegeria:** SYNTYPE, MCZ 26363; United States: [Massachusetts, Dorchester and Cambridge, Harris no. 702]; *Synanthedon pyri* (Harris); Missing abdomen.

scitula Harris, 1839: 313, **Aegeria:** SYNTYPES (2 adults, 1 pupal shell), MCZ 26362; United States: [Harris no. 333]; *Synanthedon scitula* (Harris).

syringae Harris, 1839: 311, **Aegeria:** LECTOTYPE male, MCZ 26360; United States: [Harris no. 464]; *Podosesia syringae* (Harris); One male and one female paralectotype, MCZ 26360. Lectotype designated by Purrington and Nielsen (1987: 551).

tibiale Harris, 1839: 309, **Trochilium:** SYNTYPE female, MCZ 26355; United States: New Hampshire, [Dublin], L. W. Leonard [Harris no. 387]; *Sesia tibialis* (Harris).

tricincta Harris, 1839: 310, **Aegeria:** SYNTYPES (1 male, 1 female), MCZ 26357; United States: [Harris no. 322]; *Paranthrene tabaniformis* (Rottemburg).

SUPERFAMILY COSSOIDEA

Family Cossidae

"crepera Harris, 1833: 591, **Cossus":** "SYNTYPE" male, MCZ 26393; United States: New Hampshire, [Dublin, L. W. Leonard, Harris no. 582]; *Prionoxystus robiniae* (Peck); The original description of *crepera* is generally cited as Harris (1935a: 592; 1835b: 72), but it is only listed there (as *Cossus crepera*), not described or illustrated. The first description seems to be that of Packard (1864c: 388) as *Xyleutes crepera*.

SUPERFAMILY TORTRICOIDEA

Family Tortricidae (including Cochylidae)

allutana Zeller, 1875: 295, fig. 27, **Grapholitha:** SYNTYPES (2), MCZ 14325, United States: New York, 7-1-, Speyer, and Texas, Dallas, Boll; *Episimus* [illegible] *ana* (Clemens).

amphorana Walsingham, 1879: 63, pl. LXXIV, fig. 9, **Semasia:** SYNTYPES (2), MCZ 15006; United States: Oregon, John Day River, Camp Watson, April, Walsingham; *Phaneta amphorana* (Walsingham).

angleseana Kearfott, 1907a: 64, **Enarmonia;** PARALECTOTYPE, MCZ 15014; United States: New Jersey, Anglesea, V-00 (?), W. D. Kearfott; *Grapholita angleseana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 398); see also Heinrich (1926: 31).

bobana Kearfott, 1907a: 26, **Eucosma;** PARALECTOTYPE, MCZ 14322; United States: Texas, Harris County, 7-5-1899; Described from three syntypes. Heinrich (1923: 103) designated the Salida, Colorado, specimen as lectotype; it is in USNM, not AMNH as he indicated. The third specimen, from Southwest Colorado, is in AMNH (Klots, 1942: 399). See also Powell (1968:10).

bolanderana Walsingham, 1879: 42, pl. LXIX, fig. 10, **Paedisca;** SYNTYPE, MCZ 15003; United States: California, Mount Shasta, August 1871, Walsingham; *Eucosma bolanderana* (Walsingham); Missing abdomen.

cockerellana Kearfott, 1907a: 71, **Tortrix;** PARALECTOTYPE, MCZ 14320; United States: Colorado, Glenwood Springs, September 1899; *Argyrotaenia cockerellana* (Kearfott); Lectotype male in AMNH designated by Powell (1964: 225).

constrictana Zeller, 1875: 305, fig. 36, **Paedisca;** HOLOTYPE male, MCZ 14335; United States: Texas, Dallas, Boll; *Sonia constrictana* (Zeller).

desertana Zeller, 1875: 306, fig. 37, **Paedisca;** LECTOTYPE male, MCZ 14338; United States: Texas, Dallas, Boll; *Epiblema desertana* (Zeller); Lectotype designated by Miller (1976: 50).

dietziana Kearfott, 1907a: 92, **Epinotia;** PARALECTOTYPES (2), MCZ 14302; United States: Pennsylvania, Hazleton, W. G. Dietz; *Rhopobota dietziana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 401); see also Heinrich (1923: 191).

dodana Kearfott, 1907a: 27, **Eucosma;** PARALECTOTYPE, MCZ 15019, United States: SW Colorado, 7-13-1889, W. G. Dietz; Missing abdomen. Lectotype in AMNH designated by Klots (1942: 401); see also Heinrich (1923: 106).

dodecana Zeller, 1875: 311, fig. 40, **Paedisca;** SYNTYPES (5), MCZ 14341; United States: Texas, Dallas, Boll; *Pelochrista scintillana* (Clemens).

eclipsana Zeller, 1875: 298, fig. 29, **Grapholitha** [sic]; HOLOTYPE male, MCZ 14328; United States: Texas, Dallas, Boll; Missing abdomen.

ednana Kearfott, 1907c: 161, pl. VIII: fig. 13, **Phalonia;** PARALECTOTYPES (2), MCZ 15017; United

States: Pennsylvania, Hazleton; *Anopina ednana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 417).

exasperatana Zeller, 1875: 238, **Tortrix;** SYNTYPES (2), MCZ 14309; United States: Texas, Dallas, Boll; *Platynota exasperatana* (Zeller).

fagigemmaeana Chambers, 1878b: 74, **Exartema;** SYNTYPE, MCZ 15007; United States: Kentucky, Chambers; *Olethreutes fagigemmaeana* (Chambers); Wings only, plus pupal case. Chambers refers to a single specimen in the MCZ, but then describes both sexes.

fragariana Packard, 1869: 335, **Lozotaenia;** SYNTYPE, MCZ 14315; United States: Maine; *Clepsis persicana* (Fitch); Missing abdomen.

frigidana Packard, 1856: 57, **Penthina;** LECTOTYPE male, MCZ 14306; Canada: Labrador; *Apotomis frigidana* (Packard); This species was described from two syntypes. Adamski and Peters (1986: 664) designated the lectotype (Code, Art. 74(b)). The male paralectotype is also in MCZ.

frustrana Comstock, 1880: 236, **Retinia;** PSEUDOTYPES (23+), MCZ 30298; United States: Massachusetts, Nantucket Island, S. H. Scudder; *Rhyacionia frustrana* (Comstock); The name *Retinia frustrana* was published by both Comstock (1880) and Scudder (1883). These specimens are Scudder's invalid type series. The lectotype in USNM designated by Miller (1967: 591).

fulvifrontana Packard, 1866: 59, **Penthina;** SYNTYPES (2), MCZ 14305; Canada: Labrador; *Olethreutes septentrionana* (Curtis).

glaucofuscana Zeller, 1875: 245, **Conchylis;** HOLOTYPE female, MCZ 14303; United States: Texas, Dallas, Boll.

gomonana Kearfott, 1907b: 78, **Eucosma;** PARALECTOTYPE, MCZ 15021; United States: New Jersey, Essex County, 5-11-1900, W. D. Kearfott; Lectotype in AMNH designated by Klots (1942: 403); see also Heinrich (1923: 119).

haimbachiana Kearfott, 1907a: 51, **Epinotia;** PARALECTOTYPE, MCZ 14300; United States: Pennsylvania, Philadelphia, VI-23-1904, F. Haimbach; *Gypsonoma haimbachiana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 403); see also Heinrich (1923: 163).

inimicella Zeller, 1872: 559, fig. 20, **Galleria;** HOLOTYPE male, MCZ 14275; United States: Texas, Dallas, Boll; *Pseudogalleria inimicella* (Zeller).

leucophaleratana Packard, 1866: 56, **Pandemis;** SYNTYPE, MCZ 14331; Canada: Labrador; *Ancylis tineana* (Huebner).

longipalpana Powell, 1985: 67, **Syllonoma;** HOLOTYPE male; United States: South Carolina, Horry County, Myrtle Beach, 9 July 1943, C. T. Parsons.

marcidana Zeller, 1875: 260, **Phoxopteris;** SYNTYPE male, MCZ 14330; United States: Texas, Dallas, Boll; *Ancylis platanana* (Clemens).

merrickanum Kearfott, 1907c: 156, pl. VIII, fig. 1, **Exartema;** PARALECTOTYPE, MCZ 15016; United States: Pennsylvania, New Brighton, VII-5-1904, H. D. Merrick; *Olethreutes merrickana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 405); see also Heinrich (1926: 149).

miscana Kearfott, 1907a: 91, **Eucosma;** LECTOPARATYPE, MCZ 15020; United States: California, Placer County, Cisco; *Epinotia miscana* (Kearfott); Lectotype in AMNH designated by Klots (1942).

murina Packard, 1867:60, **Penthina;** LECTOTYPE male, MCZ 14307; Canada: Labrador, Caribou Island; *Olethreutes metallicana* (Huebner); Lectotype designated by Miller (1985: 410); also paralectotype male.

nebulosana Packard, 1866: 61, **Grapholitha;** SYNTYPE male, MCZ 14312; Canada: Labrador; *Gypsonoma nebulosana* (Packard); An additional MCZ specimen may be a syntype. Heinrich (1923: 261) cites a male "type" in the Fernald collection.

niveosana Packard, 1866: 55, **Sciaphila;** SYNTYPES (6), MCZ 14313; Canada: Labrador; *Eana niveosana* (Packard).

numerosana Zeller, 1876: 317, **Paedisca;** HOLOTYPE male, MCZ 14339; United States: Texas, Dallas, Boll; *Epiblema numerosana* (Zeller).

ochromediana Kearfott, 1907a: 11, **Olethreutes;** PARALECTOTYPE, MCZ 14332; United States: Pennsylvania, Hazleton, 6/21/1902; *Olethreutes osmundana* (Fernald); Lectotype in AMNH designated by Heinrich (1926: 170).

olivaceana Fernald, 1882: 71, **Eccopsis;** PARALECTOTYPES (2), MCZ 14334; United States: [no data]; *Olethreutes olivaceana* (Fernald); Lectotype in USNM designated by Miller (1970: 292).

osmundana Fernald, 1879: 156, **Penthina;** PARALECTOTYPE, MCZ 15010; United States: Maine, Orono, feeding on *Osmunda regalis*, emerged 1 July 1879, A. Allen; *Olethreutes osmundana* (Fernald); Lectotype in USNM designated by Miller (1970. 292).

packardi Zeller, 1875: 300, fig. 31, **Grapholitha** [sic]; HOLOTYPE, MCZ 14329; United States: Texas, Dallas, Boll; Missing abdomen.

peculiana Zeller, 1875: 210, fig. 1, **Teras;** HOLOTYPE female, MCZ 14316; United States: Texas, Dallas, Boll; *Acleris subnivana* (Walker).

perfluana Zeller, 1875: 299, fig. 30, **Grapholitha** [sic]; HOLOTYPE female, MCZ 14327; United States: Texas, Dallas, Boll; *Sereda tautana* (Clemens).

pinatubana Kearfott, 1905: 9, **Eulia;** PARALECTOTYPE, MCZ 14344; United States: Massachusetts, Winchendon, V-26-1902; *Argyrotaenia pinatubana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 415).

plumbolineana Kearfott, 1907a: 53, **Epinotia;** PARALECTOTYPE, MCZ 14301; Canada: British Columbia, Wellington; Lectotype in AMNH designated by Klots (1942).

primulana Walsingham, 1879: 45, pl. LXX, fig. 7, **Paedisca;** SYNTYPE, MCZ 15004; United States: California, Mendocino County, 10 June 1871, Walsingham; *Eucosma primulana* (Walsingham).

prosperana Kearfott, 1907b: 128, **Enarmonia;** PARALECTOTYPE, MCZ 15013; United States: California, San Luis Obispo, III-[no year], A. H. Vachell; *Cydia prosperana* (Kearfott); Lectotype in AMNH designated by Klots (1942: 408); see also Heinrich (1926: 57).

ptychogrammos Zeller, 1875: 213, **Teras hastiana** variety; HOLOTYPE male, MCZ 14317; United States: Texas, Dallas, Boll; *Acleris ptychogrammos* (Zeller); Missing abdomen and hindwings.

quintana Zeller, 1875: 304, figs. 34, 35, **Paedisca;** SYNTYPES (2), MCZ 14340; United States: Texas, Dallas, Boll; *Eucosma robinsonana* (Grote).

raracana Kearfott, 1907a: 44, **Thiodia;** PARALECTOTYPE, MCZ 14326; United States: [no locality], ["8-12-99"]; *Phaneta raracana* (Kearfott); Lectotype in AMNH designated by Heinrich (1923: 41).

seriatana Zeller, 1875: 244, **Conchylis;** HOLOTYPE male, MCZ 14304; United States: Texas, Dallas, Boll; *Aethes seriatana* (Zeller).

sescuplana Zeller, 1875: 220, **Tortrix;** SYNTYPES (4), MCZ 14314; United States: Texas, Dallas, Boll; *Clepsis virescana* (Clemens).

spaldingana Kearfott, 1907a: 19, **Eucosma;** PARALECTOTYPE, MCZ 14321; United States: Utah, Stockton, "VII-26-3", T. Spaulding; Lectotype in AMNH designated by Klots (1942: 410); see also Heinrich (1923: 84).

spiculana Zeller, 1875: 289, fig. 23, **Grapholitha;** HOLOTYPE female, MCZ 14324, United States: Texas, Dallas, Boll; *Phaneta spiculana* (Zeller); Missing abdomen and right forewing.

terracoctana Walsingham, 1879: 39, **Paedisca;** SYNTYPE, MCZ 15005, United States: California, Mount Shasta; *Epinotia terracoctana* (Walsingham); This species was described from 7 syntypes from Mount Shasta. Six syntypes and an additional 24 specimens from Mount Shasta and Mendocino City are now in the BMNH. Like other Walsingham California syntypes in the MCZ, this specimen does not bear labels in Walsingham's own handwriting, but was presumably received by Chambers.

tessellana Packard, 1866: 58, **Penthina;** SYNTYPES (6), MCZ 14308; Canada: Labrador; *Olethreutes intermistana* (Clemens).

testulana Zeller, 1875: 241, **Cenopis;** HOLOTYPE male, MCZ 14311; United States: Texas, Dallas, Boll; *Sparganothis directana* (Walker).

trifurculana Zeller, 1875: 226, **Tortrix;** SYNTYPE, MCZ 14319; United States: Texas, Dallas, Boll; *Argyrotaenia quercifoliana* (Fitch); Missing left forewing.

tripartitana Zeller, 1875: 308, fig. 39, **Paedisca;** HOLOTYPE female, MCZ 14337 United States: Texas, Dallas, Boll; *Epiblema tripartitana* (Zeller).

tristriata Kearfott, 1907a: 67, **Sparganothis;** SYNTYPE, MCZ 14310; United States: Minnesota, Duluth, ["15. Fern/new"]; Missing right forewing, 1 cotype in AMNH (Klots, 1942: 416).

variolana Zeller, 1875: 212, **Teras;** HOLOTYPE male, MCZ 14318; United States: Texas, Dallas, Boll; *Acleris minuta* (Robinson).

vertumnana Zeller, 1875: 310, **Paedisca;** LECTOTYPE female, MCZ 14336; United States: Texas, Dallas, Boll; *Epinotia vertumnana* (Zeller); Lectotype designated by Brown (1987: 343).

verutana Zeller, 1875: 247, **Bactra lanceolana** variety; SYNTYPES (2), MCZ 14333; United States: Texas, Dallas, Boll; *Bactra verutana* Zeller.

vestaliana Zeller, 1875: 286, fig. 21, **Grapholitha** [sic]; HOLOTYPE male, MCZ 14323; United States: Texas, Dallas, Boll; *Hystrichophora vestaliana* (Zeller); The holotype is a male, not a female as stated by Zeller.

vitivorana Packard, 1869: 336, pl. 8, fig. 22, **Penthina;** SYNTYPE, MCZ 15008; United States: Ohio, Hudson, M. C. Reed; *Endopiza viteana* Clemens; Missing abdomen and right hindwing.

worthingtoniana Fernald, 1878: 83, **Paedisca;** SYNTYPE, MCZ 14342; United States: "North Illinois", [June], C. E. Worthington; *Eucosma bipunctella* (Walker).

zana Kearfott, 1907a: 61, **Enarmonia;** PARALECTOTYPE, MCZ 15015; Canada: British Columbia, Wellington, VI-[no year], T. Bryant; *Grapholita caeruleana* Walsingham; Lectotype in AMNH designated by Klots (1942: 412); see also Heinrich (1926: 31).

SUPERFAMILY ZYGAENOIDEA

Family Zygaenidae

sanborni Packard, 1864a: 32, **Harrisina;** HOLOTYPE [?], MCZ 27316; United States: Virginia, Alexandria, J. O. Treat; *Acoloithus falsarius* Clemens; This may not be the holotype, which was "loaned . . . by Mr. Sanborn."

Family Limacodidae

bifida Packard, 1864c: 338, **Euclea;** SYNTYPES [?] (2 males), MCZ 16028; United States: Maine, Brunswick, "at light", August; *Euclea delphinii* (Boisduval).

biguttata Packard, 1864c: 341, **Limacodes;** SYNTYPE, MCZ 26382; United States: Pennsylvania [Harris no. 753]; *Apoda biguttata* (Packard); Two additional Harris specimens may be syntypes.

cinereum Forbes, 1942: 389, **Palaeophobetron;** HOLOTYPE male, MCZ 26268; Panama: Canal Zone, Barro Colorado Island, 31 December 1934, [A. Friedman]; Label states collector was A. Friedman, not M. Bates as stated by Forbes.

ephippiatus Harris, 1869: 301, pl. I, fig. 7, pl. II, fig. 10, **Limacodes;** SYNTYPES (2 males, 2 females, 3 pupal cases), MCZ 33259; United States; "probably from Pennsylvania", T. Hill [Harris no. 775]; *Acharia stimulea* (Clemens) (see Becker and Miller, 1989).

ferruginea Packard, 1864c: 338, **Euclea;** HOLOTYPE female, MCZ 16027; United States: "St. Catharines, C. W. (Coll. Scudder)"; *Euclea delphinii* (Boisduval); Specimen is a female, not a male as stated by Packard.

geminata Packard, 1864c: 343, **Cyrtosia;** SYNTYPE male, MCZ 16031; United States: Maryland, Janesville, R. Stratton; *Packardia geminata* (Packard); Packard (1964) and Tietz ([1952]: 151) record syntype(s) from Philadelphia in ANSP.

monitor Packard, 1864c: 337, **Euclea;** SYNTYPES (2 males), MCZ 16029; United States: Massachusetts, Cambridge and Boston; *Euclea delphinii* (Boisduval); Additional 2 male, 2 female syntypes in Harris Collection.

testacea Packard, 1864c: 348, **Tortricidia;** SYNTYPES (2), MCZ 26384; United States: [Harris no. 315].

y-inversa Packard, 1864c: 341, **Limacodes;** HOLOTYPE, MCZ 26383; United States: Pennsylvania [Harris no. 781]; *Apoda y-inversa* (Packard); A pseudotype in main collection, MCZ 16030.

Family Megalopygidae

crispata Packard, 1864c: 335, **Lagoa;** SYNTYPES (1 male, 1 female), MCZ 27315; United States: Massachusetts, Brookline, C. A. Shurtleff; *Megalopyge crispata* (Packard); Packard notes "thirteen specimens reared from the blackberry bush by Mr. Shurtleff."

immaculata Cassino, 1928: 91, **Lagoa;** HOLOTYPE male, MCZ 32865; United States: Texas, Davis Mountains, 1–7 February 1926, O. C. Poling; *Megalopyge immaculata* (Cassino); Probably a synonym of *Megalopyge laycei* (Barnes and McDunnough).

pulla Forbes, 1942: 401, **Trosia;** HOLOTYPE female, MCZ 26269; Panama: Canal Zone, Barro Colorado Island, 10 October 1934, M. Bates.

SUPERFAMILY PYRALOIDEA

Family Pyralidae

albiplagiatella Packard, 1873b: 269, **Myelois;** SYNTYPES (2 males of 2), MCZ 14291; United States: New Hampshire, May and June, C. A. Walker; *Pima albiplagiatella* (Packard).

anticostalis Grote, 1871: 104, **Botys;** SYNTYPES (1 male, 1 female), MCZ 14263; United States: Alabama, "about Demopolis"; *Eulepte anticostalis* (Grote).

argillaceellus Packard, 1867: 54, **Crambus;** SYNTYPES (2), MCZ 14295; Canada: Labrador, Square Island, 14 July 1864; *Raphiptera argillaceella* (Packard).

betulella Hulst, 1890: 125, **Aerobasis;** PARALECTOTYPE female, MCZ 14284; United States: New York, July; Lectotype in AMNH designated by Neunzig (1986: 59).

borealis Packard, 1867: 53, **Pyrausta;** HOLOTYPE female, MCZ 14270; Canada: Labrador, Square Island, 14 July [1864]; *Pyrausta subsequalis borealis* Packard.

caeculalis Zeller, 1875: 333, pl. 10: fig. 46, **Perispasta;** HOLOTYPE male, MCZ 14259; United States: Texas, Dallas, Boll.

californicalis Packard, 1873a: 264, **Eromene;** LECTOTYPE male, MCZ 14297; United States: California, H. Edwards; *Euchromius californicalis* (Packard); Capps (1966: 5) saw two of the three males now in the collection, and designated one of the two as lectotype, without so labelling it. Since there are three specimens, not two, it is not clear which one is the lectotype. One of the three may not be a syntype because it was collected by Behrens, not Edwards.

carpenterellus Packard, 1874: 548, fig. 1, **Crambus;** SYNTYPES (4 of 8), MCZ 14299, United States: Colorado, "Mountains of Colorado", 19 July, 12 August, and 8 September 1873, W. L. Carpenter; *Crambus hamellus carpenterellus* Packard; Brown (1972: 247) restricted the type locality to Weston Pass, Park County, Colorado.

comptoniella Hulst, 1890: 125, **Acrobasis;** LECTOTYPE male, MCZ 14283; United States: New York, Long Island, July; Lectotype designated by Neunzig (1986: 56).

consobrinella Zeller, 1872: 548, **Nephopteryx;** HOLOTYPE male, MCZ 14287; United States: Texas, Dallas, Boll; *Glyptocera consobrinella* (Zeller).

cuprina Zeller, 1872: 497, **Aglossa;** SYNTYPES (1 male, 1 female), MCZ 14257; United States: Texas, Dallas, Boll.

decimerella Hulst, 1888: 117, **Lipographis;** Probable SYNTYPE female, MCZ 14288; United States: Texas, Blanco County, August; *Stylopalpia scobiella* (Grote).

edmandsii Packard, 1864b: 120, **Nephopteryx;** SYNTYPE, MCZ 14278; United States: Massachusetts; *Vitula edmandsii* (Packard).

electella Hulst, 1887: 137, **Anerastia;** Probable SYNTYPE, MCZ 14279; United States: Texas, Blanco County; *Homoeosoma electella* (Hulst).

fenestrella Packard, 1873a: 259, **Pempelia;** SYNTYPES (2 of 6), MCZ 14292; United States: California, H. Edwards; *Lipographis fenestrella* (Packard); Edwards number 711 indicates Angel Island, April.

feriella Hulst, 1888: 115, **Tacoma;** Probable SYNTYPE, MCZ 14286; United States: Texas, [Blanco County, August].

feudalis Grote, 1875: 231, **Botis;** SYNTYPE, MCZ 16095, United States: New York and Massachusetts; *Herpetogramma thesceusalis* (Walker).

frigidella Packard, 1867: 53, **Eudorea;** SYNTYPE, MCZ 14296, Canada: Labrador, Caribou Island; *Pyla fusca* (Haworth); Abdomen missing.

fulminalis Zeller, 1872: 560, fig. 19, **Melissoblaptes;** HOLOTYPE male, MCZ 14276; United States: Texas, Dallas, Boll, *Paralipsa fulminalis* (Zeller).

glacialis Packard, 1867: 52, **Botys;** HOLOTYPE female, MCZ 15354, Canada: Labrador, Hopedale, 5 August 1864, *Udea inquinatalis* (Zeller). Packard (1867) indicates one sex only and no range of size.

hospitella Zeller, 1875: 338, **Ephestia;** PARALECTOTYPES (6), MCZ 14277, United States: Texas, Dallas, Boll; *Eurythmia hospitella* (Zeller). Lectotype in BMNH designated by Heinrich (1956: [illegible]).

integra Zeller, 1873: 328, fig. 44, **Scoptonoma;** SYNTYPES (3), MCZ 16094; United States: Texas, Dallas, Boll; *Lineodes integra* (Zeller); Although labelled as types by Hagen, these specimens were probably not seen by Zeller, who described the species from "Ein paar in meiner Sammlung, mehrere nach Hagens Angabe im Cambridger Museum."

interrupta Zeller, 1873: 329, **Scoptonoma;** SYNTYPES (4), MCZ 16093; United States: Texas, Dallas, Boll; Lineodes interrupta (Zeller); As with *Scoptonoma integra* above, Zeller probably did not see these specimens.

latifasciatella Packard, 1873b: 269, **Nephopteryx;** HOLOTYPE female, MCZ 14290; United States: Maine, A. S. Packard; *Telethusia ovalis* (Packard).

leoninella Packard, 1873a: 259, **Pempelia;** SYNTYPES (2 of 3), MCZ 14293; United States: California, H. Edwards; *Lipographis leoninella* (Packard); Edwards number 706 indicates San Mateo County, pastures, May.

lentifluualis Zeller, 1872: 525, **Homophysa;** SYNTYPE, MCZ 14274; United States: Texas, Dallas, Boll; *Aethiophysa lentifluualis* (Zeller).

melanogrammos Zeller, 1872: 546, fig. 24, **Tetralopha;** HOLOTYPE male, MCZ 14256; United States: Texas, Dallas, Boll; Specimen illustrated by Holland and Schaus (1925: 65).

metalliferalis Packard, 1873a: 265, **Calaclysta;** SYNTYPES (2 of 4), MCZ 33257; United States: California, H. Edwards; *Dicymolomia metalliferalis* (Packard); Edwards number 208 indicates San Mateo County, marshy places, May.

mustelinalis Packard, 1873a: 262, **Botys;** SYNTYPES (2 of 2), MCZ 14269; United States: California, H. Edwards; *Mecyna mustelinalis* (Packard); One specimen has Edwards number 773 indicating Angel Island, May.

occidentalis Packard, 1873a: 260, **Scopula;** LECTOTYPE female, MCZ 14264; United States: California, H. Edwards; *Achyra occidentalis* (Packard); Lectotype designated by Capps (1967: 51). Edwards number 716 indicates Point Lobos, pastures, May.

ochrifrontella Zeller, 1875: 337, **Ephestia;** HOLOTYPE male, MCZ 14280; United States: Texas, Dallas, Boll; *Eulogia ochrifrontella* (Zeller).

octonalis Zeller, 1873: 211, **Orobena;** HOLOTYPE male, MCZ 14273; United States: Texas, Dallas, Boll; "*Lygropia*" *octonalis* (Zeller) (needs new genus according to Munroe, pers. comm.).

ovalis Packard, 1873b: 269, **Pempelia;** HOLOTYPE, MCZ 14289; United States: Maine, A. S. Packard; *Telethusia ovalis* (Packard); Missing abdomen.

perrubralis Packard, 1873a: 264, **Botys;** SYNTYPES (2 of 3), MCZ 14267; United States: California; *Pyrausta perrubralis* (Packard).

plumbicostalis Grote, 1871: 103, **Botys;** HOLOTYPE male, MCZ 32943; United States: Alabama, "about Demopolis"; *Lygropia plumbicostalis* (Grote); Prothorax, left forewing, and right wings only.

profundalis Packard, 1873a: 261, **Botys;** SYNTYPES (2 of 5), MCZ 14271; United States: California, H. Edwards; *Udea profundalis* (Packard); Edwards number 705 indicates San Mateo County, pastures, May.

reniculalis Zeller, 1872: 526, **Homophysa;** SYNTYPE male, MCZ 14261; United States: Texas, Dallas, Boll; *Nephrogramma reniculalis* (Zeller).

roseatella Packard, 1873b: 270, **Nephopteryx;** LECTOTYPE male, MCZ 14282; United States: Massachusetts, Dorchester, F. G. Sanborn; *Peoria approximella* (Walker); Lectotype, and paralectotype also in MCZ, designated by Shaffer (1968: 30).

rubrifasciella Packard, 1873b: 267, **Acrobasis;** SYNTYPES (4 of 15), MCZ 14285; United States: Maine, Orono, A. S. Packard; See Neunzig (1986: 57) for discussion of identity of types.

semirubralis Packard, 1873a: 263, **Botys;** HOLOTYPE male, MCZ 14268; United States: California, [Sausalito, 6 May 1872], H. Edwards, *Pyrausta semirubralis* (Packard); A second male from "S. Nevada" (Sierra Nevada Mountains of California) is also labelled "type" in Packard's handwriting, but is probably not the holotype, since there are other specimens in the MCZ with the same data but without type labels.

serratissimalis Zeller, 1872: 521, **Crocidophora;** PARALECTOTYPE female, MCZ 14262; United States: Texas, Dallas, Boll; Lectotype in BMNH designated by Monroe (1976: 22).

sesquialteralis Zeller, 1873: 209, fig. 5, **Botis;** HOLOTYPE male, MCZ 32924; United States: Texas, Dallas, Boll; *Microtheoris o. ophionalis* (Walker).

sincera Zeller, 1875: 332, **Oectoperia;** SYNTYPES (2 of 2), MCZ 14258; United States: Texas, Dallas, Boll; *Salobrena sincera* (Zeller).

subdivisalis Grote, 1871: 126, **Desmia;** HOLOTYPE [?], MCZ 14260; United States: Alabama, "about Demopolis"; Specimen consists of right wings only.

subolivalis Packard, 1873a: 261, **Botys;** SYNTYPES (2), MCZ 14266; United States: Maine, Brunswick, in grass uplands, and Orono, Maine, A. S. Packard, Jr.; *Pyrausta unifascialis subolivalis* (Packard).

tetradella Zeller, 1872: 552, **Anerastia;** PARALECTOTYPES (2), MCZ 14281; United States: Texas, Dallas, Boll; *Peoria tetradella* (Zeller); Lectotype in BMNH designated by Shaffer (1968: 17).

unifascialis Packard, 1873a: 261, **Botys;** SYNTYPES (2 of 2), MCZ 14265; United States: California, H. Edwards; *Pyrausta unifascialis* (Packard); Klots (1942: 422) designated a lectotype and paralectotype in AMNH. However, the MCZ specimens are probably the real types, since Packard kept the other types of California Pyralidae from Edwards. Beutenmueller (1892: 196) listed one type in AMNH.

unistriatellus Packard, 1867: 54, **Crambus;** SYNTYPE male, MCZ 22641; Canada: Labrador, Caribou Island.

vibicalis Zeller, 1873: 208, fig. 4, **Botis;** HOLOTYPE male, MCZ 14272; United States: Texas, Dallas, Boll; *Microtheoris vibicalis* (Zeller) (see Munroe, 1972: 147, about misspelling of name as *ribicalis*).

Family Thyrididae

dimidiata Forbes, 1942: 345, **Rhodoneura;** HOLOTYPE female, MCZ 26263; Panama: Barro Colorado Island, 2-XII-1934, M. Bates; Missing abdomen.

longalis Forbes, 1942: 340, **Dysodia;** HOLOTYPE male, MCZ 26264; Panama: Barro Colorado Island, 29-XI-1934, M. Bates.

maculata Harris 1839: 313, **Thyris;** SYNTYPES (4), MCZ 26346; United States: [New Hampshire, Harris no. 219]; All missing abdomens.

mesogramma Forbes, 1942: 341, **Ochrothyris;** HOLOTYPE male, MCZ 26265; Panama: Barro Colorado Island, 10-I-1935, A. Friedman.

SUPERFAMILY PTEROPHOROIDEA
Family Pterophoridae

cervinidactylus Packard, 1873a: 266, **Pterophorus;** HOLOTYPE, MCZ 1785; United States: California, H. Edwards; *Platyptilia pallidactyla* (Haworth); Missing right wings and abdomen.

cineraceus Fish, 1881: 73, **Oidaematophorus;** SYNTYPE male, MCZ 1781; United States: Washington Territory, H. K. Morrison; Barnes and Lindsey (1921: 392) consider this specimen a paratype.

grandis Fish, 1881: 141, **Lioptilus;** "LECTOTYPE" male, MCZ 1782; United States: California; *Oidaematophorus grandis* (Fish); Cashatt (1972: 5) designated this specimen as lectotype, unaware of a previous lectotype designation by Klots (1942: 423) of a female in the AMNH.

lacteodactylus Chambers, 1873: 72, **Pterophorus;** HOLOTYPE male, MCZ 1783; United States: Kentucky, Chambers; *Oidaematophorus lacteodactylus* (Chambers); Missing abdomen.

paleaceus Zeller, 1873: 326, **Leioptilus;** SYNTYPES

♂, MCZ 1787; United States: Texas, Dallas, Boll; *Oidaematophorus paleaceus* (Zeller).

pergracilidactylus Packard, 1873a: 265, **Pterophorus:** HOLOTYPE, MCZ 1786; United States: California, H. Edwards; *Emmelina monodactyla* (Linnaeus); Missing left wings and abdomen.

pumilio Zeller, 1873: 324, **Mimesoptilus:** HOLOTYPE male, MCZ 1788; United States: Texas, Dallas, Boll; *Marasmarcha pumilio* (Zeller).

semicostatus Zeller, 1873: 323, **Mimeseoptilus:** SYNTYPES (2 of 2), MCZ 1789; United States: Texas, Dallas, Boll; *Stenoptilia zophodactyla* (Duponchel); One male and one female, although Zeller stated two males.

sulphureodactylus Packard, 1873a: 266, **Pterophorus:** SYNTYPES (6 of 8), MCZ 1784; United States: California, Siskiyou County, Goose Lake, 26–27 July, J. Holleman; *Oidaematophorus sulphureodactylus* (Packard).

APPENDIX

Chambers "types" in the British Museum (Natural History)

The collection of the BMNH contains specimens sent by Chambers to Stainton in the 1870s. Some of them probably are syntypes of Chambers' species, others are not syntypes but are topotyes, and others are taxa described by other authors. The topotypes might prove useful to document Chambers' species concepts, or as neotype candidates.

There are three lots of Chambers specimens now in the Stainton collection. The August 1877 shipment to Stainton was accompanied by the following letter from Chambers:

"Wishing to preserve types of species of Tineina described by me, and likewise to make some acknowledgement . . . it has been my intention to send you as complete a collection of the species of this region [Covington, Kentucky] as I could make. Unfortunately during my absence in Colorado more than half the collection that I had made before I went there was destroyed and the remainder with a small collection that I made in Colorado, was sent to the . . [MCZ]. This spring and summer I have attempted to supply a few cabinets in this country and your own. Unfortunately the continued ill–health of my son again calls me to Colorado and unwilling to risk the destruction of my collection while I am absent I distribute it — so far as I have renewed it — now. I enclose here with 67 species of Tineina and one of Tortricina."

The specimens are listed here as identified by Chambers. We have made no attempt to verify identifications. The localities listed here are those indicated by Chambers in correspondence or on labels, and are not necessarily the type localities. The first lot, sent December 1876, includes *Lithariapteryx abroniaeella* Chamber "from Colorado where the larva mines the leaves of *Abronia fragrans* up to an altitude of about 7,000 feet above sea level" and *Batrachedra praeangusta* Chambers from Colorado.

The second lot, sent in January 1877, now includes 5 species, but originally included 6.

1. *Lithariapteryx abroniaeella* Chambers Colorado
2. *Lithocolletis salicifoliella* Chambers
3. *Lithocolletis amphicarpeaeella* Chambers Kentucky
4. *Laverna magnatella* Chambers = *Laverna oenotheriella* Chambers
5. *Gracilaria* [sic] *salicifoliella* Chambers
6. *Eurynome albella* Chambers Colorado [must have been damaged in transit, not at BMNH]

The largest lot was sent in August 1877. All bear Chambers' handwritten numbers and Stainton's name labels. The numbers not cited in the following list refer to species described by authors other than Chambers.

1. *Xylesthia clemensella* Chambers Kentucky
2. *Tinea bimaculella* Chambers Kentucky
3. *Tinea caemetariiella* [sic] Chambers Kentucky
5. *Semele cristatella* Chambers Kentucky

6. *Agnippe biscolorella* Chambers Kentucky
7. *Hyponomeuta longimaculella* Chambers Kentucky
8. *Depressaria eupatoriiella* Chambers Kentucky
9. *Gelechia querciella* Chambers Kentucky
10. *Gelechia cristatella* Chambers Kentucky
11. *Gelechia rubensella* Chambers Kentucky
13. *Helice pallidochrella* Chambers Kentucky
17. *Argyresthia undulatella* Chambers Kentucky
18. *Gracilaria packardella* [sic] Chambers Kentucky
19. *Corisium albanotella* Chambers Kentucky
20. *Gracilaria* [sic] *fasciella* Chambers Kentucky
21. *Gracilaria* [sic] *purpuriella* Chambers Kentucky
23. *Coleophora ochrella* Chambers Kentucky
24. *Coleophora caryaefoliella* Chambers Kentucky
25. *Laverna cephalanthiella* Chambers Kentucky
26. *Chrysopelia purpuriella* Chambers Kentucky
27. *Laverna? gleditschiaeella* Chambers Kentucky
28. *Perimede erransella* Chambers Kentucky
30. *Dryope murtfeldtella* Chambers Kentucky
31. *Tischeria quercivorella* Chambers Kentucky
32. *Tischeria heliopsisella* Chambers Kentucky
33. *Bucculatrix luteella* Chambers Kentucky
35. *Philonome clemensella* Chambers Kentucky
36. *Phyllocnistis vitifoliella* Chambers Kentucky
37. *Phyllocnistis ampelopsiella* Chambers Kentucky
40. *Leucanthiza amphicarpeaefoliella* Chambers Kentucky
41. *Lithocolletis clemensella* Chambers Kentucky
43. *Lithocolletis fuscocostella* Chambers Kentucky
44. *Lithocolletis celtisella* Chambers Kentucky
45. *Lithocolletis cincinnatiella* Chambers Kentucky
47. *Lithocolletis ulmella* Chambers Kentucky
49. *Lithocolletis tiliacella* Chambers Kentucky
50. *Lithocolletis ornatella* Chambers Kentucky
51. *Lithocolletis corylisella* Chambers Kentucky
52. *Lithocolletis ambrosiaeella* Chambers Kentucky
53. *Polyhymno sexstrigella* Chambers Texas
54. *Perimede unomaculella* Chambers Texas
55. *Elachista parvipulvella* Chambers Texas
58. *Ornix prunivorella* Chambers Kentucky
59. *Gelechia fuscoochrella* Chambers Kentucky
60. *Lithocolletis tritaeniaella* Chambers Kentucky
61. *Nepticula apicialbella* Chambers Kentucky
63. *Gracilaria 12-lineella* Chambers Kentucky
64. *Gelechia bimaculella* Chambers Kentucky
65. *Lithocolletis corylisella* Chambers Kentucky
66. *Gelechia variiella* [sic] Chambers Kentucky
68. *Microaethia amphicarpeaeana* Chambers Kentucky

The correspondence also indicates a shipment in November 1872 which included 41 Chambers species. However, these specimens could not be located at the BMNH.

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EARLY MISSISSIPPIAN BLASTOIDS FROM WESTERN MONTANA

JAMES SPRINKLE[1] AND RAYMOND C. GUTSCHICK[2]

ABSTRACT. Several faunas of Early Mississippian blastoids occur in the Lodgepole and Allan Mountain Limestones of western Montana. More than 1,400 complete specimens representing at least nine genera and 16 species have been collected from three different zones, making this one of the largest blastoid collections known from western North America. The largest and most diverse blastoid fauna occurs just above the base of the Lodgepole (lower Paine Member) and Allan Mountain Limestones at 31 localities and consists of nearly 1,200 specimens belonging to four blastoid genera (*Tanaoblastus*, *Strongyloblastus*, *Orophocrinus*, and *Metablastus*). A second fauna occurs in the middle Lodgepole Limestone (upper Paine Member) at four localities where about 195 specimens and five blastoid genera occur (*Koryschisma*, n. gen., *Montanablastus*, n. gen., *Strongyloblastus*, *Cryptoblastus*?, and *Hadroblastus*). The highest fauna occurs near the top of the Lodgepole Limestone (upper Woodhurst Member) at three localities in the Bridger Range and is represented by 19 specimens and three blastoid genera (*Cryptoblastus*?, *Orophocrinus*, and *Phaenoschisma*).

Most of the blastoids in these faunas are fairly well silicified, and, when extracted with heated acetic acid, a few show excellent preservation of plate ornament and ambulacral structures. One blastoid occurrence in the middle Lodgepole has calcitic specimens with complete brachioles and attached stem segments that lack distal attachment structures. The Lodgepole blastoid faunas appear to be middle Kinderhookian to early Osagean (early to middle Tournaisian) in age, and are most similar to other Early Mississippian (or earliest Carboniferous) blastoid faunas in Missouri, Alberta, New Mexico, and Belgium. The diverse lower Lodgepole fauna is dominated by a small globular spiraculate (*Tanaoblastus*) at nearly all sections, whereas other pyramidal, elongate, and club-shaped spiraculate or fissiculate blastoids are much less common. Most of these blastoids were apparently attached, medium-level, suspension feeders living on a lime mud bottom in a carbonate ramp setting near or well below normal wave base. At several localities, members of the lower and middle Lodgepole blastoid faunas are found adjacent to or just below Waulsortian-type bioherms.

New taxa include the fissiculates *Koryschisma elegans*, n. gen., n. sp., and *Orophocrinus macurdai*, n. sp., and the spiraculates *Metablastus milliganensis*, n. sp., *Strongyloblastus breimeri*, n. sp., *S. laudoni*, n. sp., *Montanablastus baldyensis*, n. gen., n. sp., and *Tanaoblastus allanensis*, n. sp.

INTRODUCTION

Blastoids are usually considered a relatively rare element in the Early Mississippian faunas of the northern Rocky Mountain region in the western United States. Only four blastoid species from the Early Mississippian of this region have been described in the 120 years between 1865 and 1985. However, several authors have reported the presence of unidentified blastoids in faunal lists during this period. Between 1963 and 1968, we made an extensive collection of blastoids from the Lodgepole and Allan Mountain Limestones of Early Mississippian age in western Montana and adjacent states. This new material and a restudy of previously described specimens form the basis for this paper.

The present authors independently discovered blastoids in the Early Mississippian of western Montana during the summers of 1962 and 1963. During the following three summers (1964–66), we returned to Montana to work together on the biostratigraphy and paleontology of the Sappington Member of the Three Forks Formation and the Lodgepole Limestone under NSF-sponsored grants (see Acknowledgments; Sprinkle, 1965; Sprinkle

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TABLE 1. LIST OF COLLECTING LOCALITIES WHERE WE COLLECTED BLASTOIDS FROM THE LODGEPOLE AND ALLAN MOUNTAIN LIMESTONES IN WESTERN MONTANA AND SOUTHEASTERN IDAHO. LOCALITIES FOR BORROWED USGS SPECIMENS (SQUAW CREEK, GALLATIN RANGE; OLD BALDY, GRAVELLY RANGE; AND BRAZER →

Locality	Code	Range	Land-grid location
Antelope Valley	AV		SW, NE, NE, sec. 2, T1S, R2W
Ant Park	AP	Little Belt Mtns.	NW, SW, sec. 35, T12N, R9E
Bacon Rind Creek	BA	Gallatin Range	SE, SE, sec. 22, T10S, R5E
Baldy Mountain	BY	Bridger Range	NW, SE, sec. 11, T1S, R6E
Bandbox Mountain	BD	Little Belt Mtns.	NE, NW, sec. 20, T14N, R10E
Bridger Mountain	BG	Bridger Range	SW, NE, sec. 11, T1S, R6E
Brownback Gulch	BB	Tobacco Root Mtns.	NE, NW, SE, sec. 20, T1S, R3W
Cowboy Canyon	CB	Madison Range	SE, NW, sec. 27, T4S, R2E
Crown Mountain	CR	Lewis & Clark Mtns.	C, SW, sec. 28, T19N, R9W
Dry Hollow	DH		SW, NE, sec. 3, T1N, R1W
Dudley Creek	DC	Madison Range	NW, SE, sec. 32, T6S, R4E
Ellis Mountain (Ellis Peak)	EM	Gallatin Range	NW, SE, sec. 14, T3S, R6E
Gallop Creek	GP	Bridger Range	SE, SW, sec. 11, T3N, R5E
Grendah Mountain	GH	Little Belt Mtns.	SE, NE, NW, sec. 31, T13N, R9E
Jordan Creek	JC	Madison Range	W½, sec. 23, T5S, R1E
Little Antelope Creek	LA	Tobacco Root Mtns.	S½, sec. 27, T1S, R2W
London Hills	LH		N½, NW, sec. 4, T1S, R2W
Milligan Canyon	MC		NE, SW, sec. 36, T2N, R1W
Milligan Canyon East	MC(E)		NE, SW, sec. 31, T2N, R1E
North Frazier Lake	FR	Bridger Range	NW, SE, sec. 9, T2N, R6E
North Sawtooth Mountain	NS	Lewis & Clark Mtns.	SW, NE, sec. 13, T21N, R9W
Northeast Baldy Mountain	NB	Bridger Range	SE, SE, SE, sec. 2, T1S, R6E
Pole Canyon	PC	Tobacco Root Mtns.	SW, sec. 8, T1S, R3W
Roy Gulch	RG	Horseshoe Hills	NW, NW, sec. 28, T4N, R4E
Sacagawea Peak	SA	Bridger Range	SE, NW, sec. 27, T2N, R6E
Saddle Peak	SP	Bridger Range	E½, NE, sec. 35, T1S, R6E
Sand Creek	SC		SW, NE, sec. 4, T1S, R1W
Sixteen Mile Creek	SX	Horseshoe Hills	SE, SW, sec. 4, T4N, R3E
South Boulder	SB	Tobacco Root Mtns.	SE, SW, sec. 20, T1S, R2W
Squaw Creek Ranger Station	SQ	Gallatin Range	NW, NE, sec. 28, T4S, R4E
Standard Creek	ST	Gravelly Range	NE, SE, sec. 6, T11S, R1W
Targhee Peak	TG	Henrys Lake Mtns.	NE, SW, SW, sec. 9, T16N, R43E
Timber Butte	TB	Gallatin Range	NE, SE, sec. 11, T5S, R5E

and Gutschick, 1967; Gutschick, McLane, and Rodriguez, 1976; Sprinkle and Gutschick, 1983). This research resulted in the discovery that blastoids are relatively common and diverse in the basal part of the Lodgepole and Allan Mountain Limestones over much of western Montana and that they are also present at two higher levels in the Lodgepole. Blastoids have now been found at 33 sections (Table 1) in southwestern, west-central, and northwestern Montana and in southeastern Idaho (Text-Fig. 1), and are undoubtedly present at many other localities in western Montana and adjacent states. During these three summers of field work and shorter visits in 1967 and 1968, we collected more than 1,400 blastoid specimens, belonging to nine genera and 16 species.

PREVIOUS STUDIES OF MADISON GROUP STRATIGRAPHY

The Madison Group in western Montana is made up of the thinner-bedded Lodgepole Limestone below (Text-Fig. 2) and the overlying more massive-bedded Mission Canyon Limestone. Together these two units represent 750 ft (229 m) to more than 2,000 ft (610 m) of Early and Middle Mississippian tropical-shelf carbonates. Lodgepole thicknesses range from about

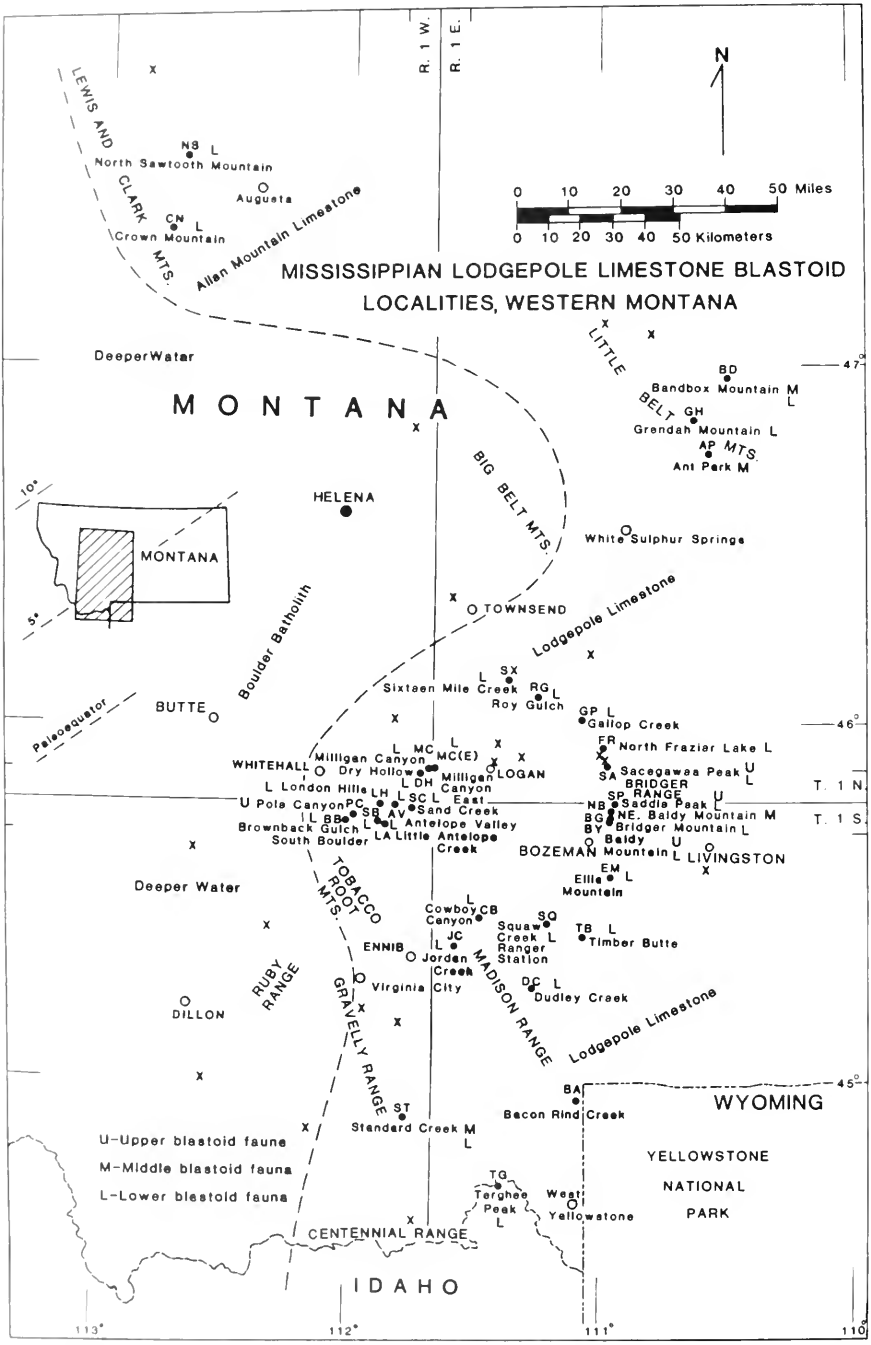
(*continued*) CANYON, NORTHERN UTAH) ARE NOT INCLUDED BECAUSE WE DID NOT VISIT OR COLLECT BLASTOIDS THERE. ABBREVIATIONS FOR BLASTOID GENERA INCLUDE: C = *CRYPTOBLASTUS*?, H = *HADROBLASTUS*, K = *KORYSCHISMA*, M = *METABLASTUS*, MO = *MONTANABLASTUS*, O = *OROPHOCRINUS*, P = *PHAENOSCHISMA*?, S = *STRONGYLOBLASTUS*, AND T = *TANAOBLASTUS*.

Topographic map	County	State	Fauna	Blastoid composition
Jefferson Island	Madison	Mont.	Lower	4 T, 1 M
Sand Point	Meagher	Mont.	Middle?	1 S, 1 K?
Tepee Creek	Gallatin	Mont.	Lower	1 T
Sedan	Gallatin	Mont.	Lower, Upper	3 T; 1 O, 1 C
Bandbox Mountain	Judith Basin	Mont.	Lower, Middle	8 T; 27 K, 4 C
Sedan	Gallatin	Mont.	Lower	8 T
Waterloo	Madison	Mont.	Lower	1 T
Ancenney	Madison	Mont.	Lower	14 T
Choteau	Lewis & Clark	Mont.	Lower	174 T
Three Forks	Jefferson	Mont.	Lower	21 O, 1 S, 1 T
Spanish Peaks	Gallatin	Mont.	Lower	1 T
Mystic Lake	Gallatin	Mont.	Lower	14 T
Maudlow	Gallatin	Mont.	Lower	10 T
King's Hill	Judith Basin	Mont.	Lower	1 T
Ennis	Madison	Mont.	Lower	10 T
Harrison	Madison	Mont.	Lower	25 T, 2 O
Jefferson Island	Madison	Mont.	Lower	220 T, 1 M
Three Forks	Jefferson	Mont.	Lower	17 S, 2 O, 1 T, 1 M
Three Forks	Broadwater	Mont.	Lower	19 S, 15 O, 5 T, 2 M
Sedan	Gallatin	Mont.	Lower	25 T
Sawtooth Ridge	Lewis & Clark	Mont.	Lower	2 T
Sedan	Gallatin	Mont.	Lower, Middle	4 T, 2 M; 29 Mo, 10 S, 1 C
Whitehall	Madison	Mont.	Upper?	1 C
Maudlow	Gallatin	Mont.	Lower	2 T
Sedan	Gallatin	Mont.	Lower, Upper	2 T; 11 C, 1 K?
Sedan	Gallatin	Mont.	Lower, Upper	1 T, 1 S; 1 P
Three Forks	Gallatin	Mont.	Lower	1 O
Toston	Broadwater	Mont.	Lower	7 T
Harrison	Madison	Mont.	Lower	2 T, 2 S
Garnet Mountain	Gallatin	Mont.	Lower	18 T
Monument Ridge	Madison	Mont.	Lower, Middle	437 T, 2 O, 1 S; 1 H
Targhee Peak	Fremont	Idaho	Lower	51 T, 1 S
Garnet Mountain	Gallatin	Mont.	Lower	8 T

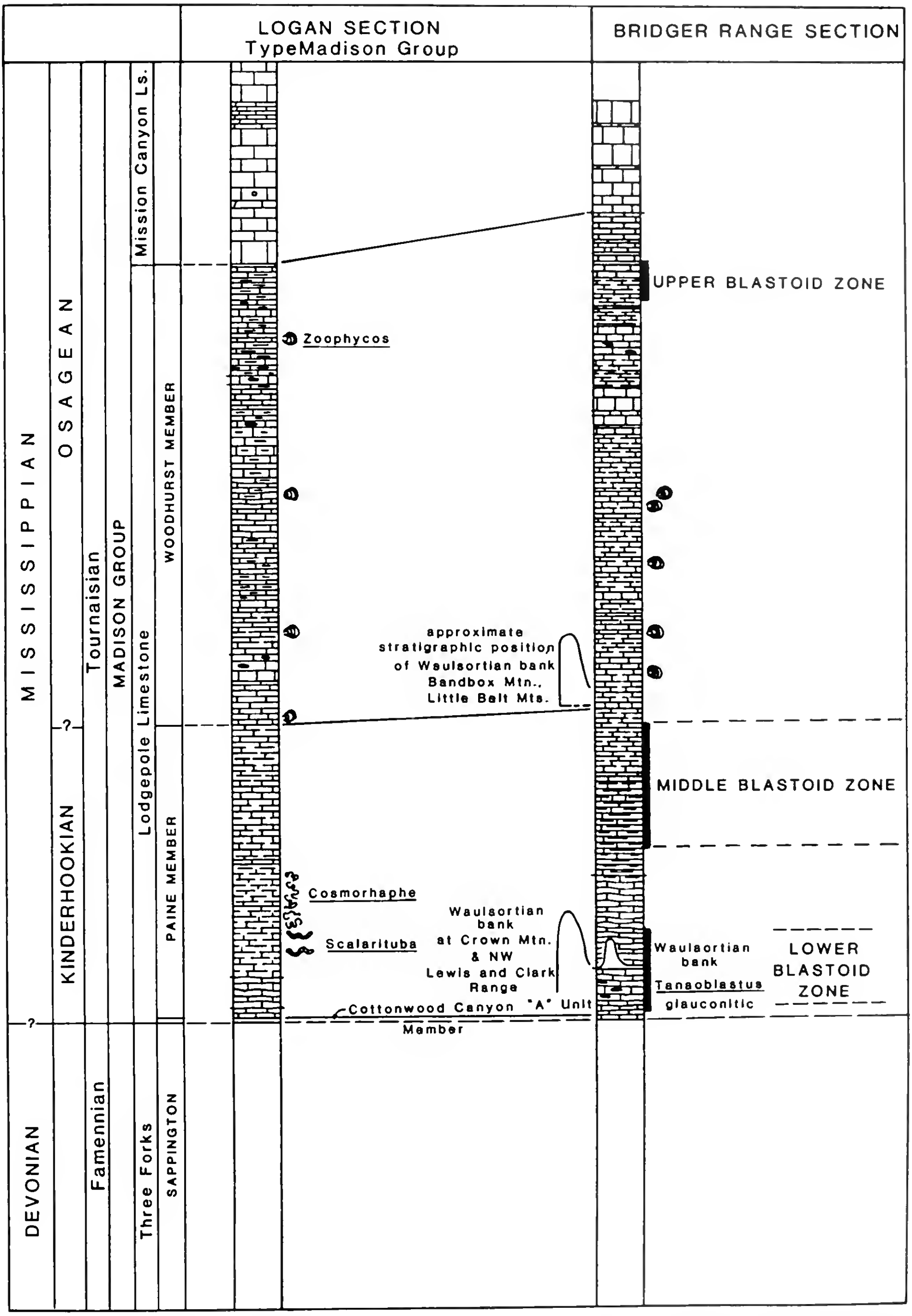
500 ft (152 m) to more than 1,000 ft (305 m) (Gutschick, McLane, and Rodriguez, 1976, pp. 107–108, figs. 8-12, 8-13). These competent structurally-deformed rocks commonly form the backbone and crest of many mountain ranges (Text-Figs. 3–6). The enormous volume of carbonate rock and the physiographic obstacles make access, observation, and collection difficult for depositional and paleontological field studies. Nevertheless, many local and regional contributions have been published for Montana.

Some useful studies of the Lodgepole Limestone which contains the blastoid faunas described here include the following: Sloss and Hamblin, 1942; Laudon and Severson, 1953; Andrichuk, 1955; Roberts, 1966; Wilson, 1969; Sando, Mamet, and Dutro, 1969; Craig, 1972; Smith, 1972, 1977; Sando and Dutro, 1974; Sando, 1976; Rose, 1976; Gutschick, McLane, and Rodriguez, 1976; Roberts, 1979; Gutschick, Sandberg, and Sando, 1980; and Sandberg and Gutschick, 1983, 1984.

Studies of the Allan Mountain Limestone in the Sun River area include: Sloss and Laird, 1945; Mudge, Sando, and Dutro, 1962; and Haines, 1977. Several occurrences of Waulsortian-like bioherms are known from the lower and middle Lodgepole Limestone and are discussed in



Text-Figure 1. Map of western Montana and adjacent states showing the location of the 33 sections (black dots) where the authors collected blastoids from the Lodgepole and Allan Mountain Limestones between 1962 and 1968. Dashed line shows boundary between fossiliferous, shallow-water environments in the lower Lodgepole Limestone to the east, and nearly unfossiliferous deeper-water environments further west. No blastoids were found at localities marked with X's.



Text-Figure 2. Generalized measured section of the Lodgepole Limestone at Logan (type section of the Madison Group) and in the Bridger Range showing where the lower, middle, and upper blastoid faunas have been found. Position of Waulsortian banks and trace fossil facies are also marked.

Text-Figure 3. View of the north flank of Sacagawea Peak (SA) in the northern Bridger Range from the peak just to the north. The Lodgepole and Mission Canyon Section was measured along the ridge on the skyline. Right arrow points to base of Lodgepole Limestone just below where *Tanaoblastus* occurs; left arrow points to beds on crest about 655 ft (200 m) above base of Lodgepole where *Cryptoblastus*? sp. A found. Zig-zag trail up to pass at back of cirque is visible in right foreground. See McMannis (1955).

Cotter, 1965, 1966; Stone, 1972; and Smith, 1977, 1982.

PRESERVATION AND PREPARATION

Nearly all of the specimens in the lower Lodgepole blastoid fauna are silicified, which made possible their discovery and collection in the field and their extraction from the surrounding limestone matrix in the laboratory. At most sections, the blastoids are very well silicified, having the endoskeleton completely replaced by silica, and even the delicate internal hydrospires are often well-preserved. In different specimens, the interior cavity of the blastoid is hollow, partly filled with secondary quartz crystals, or completely filled with cryptocrystalline chalcedony, the last condition occurring most commonly where the blastoids are closely associated with nodular chert. The blastoids appear to be one of the better silicified members of the fauna in most of the sections where they occur.

At a few sections, especially North Frazier Lake (FR) in the Bridger Range, Roy Gulch (RG) in the Horseshoe Hills, and North Sawtooth Mountain (NS) in Sun River Canyon, northwestern Montana (see Text-Fig. 1), specimens of *Tanaoblastus* are only slightly or partly silicified, making their extraction from the surrounding limestone matrix very difficult. In these specimens, the silicification occurs either as patches in the endoskeleton or as a thin skin of silica that is easily broken through during acid preparation.

Nearly all the collected blastoids that appeared to be well silicified were extracted from the surrounding limestone matrix by the use of either heated acetic acid or cold dilute hydrochloric acid. During the early stages of this project, it was discovered that many of the silicified blastoids could be recovered in much better condition by using acetic acid instead of the faster-working hydrochloric acid, and acetic acid was used in all of the later work.

Text-Figure 4. View of the southern Bridger Range taken from the southwest flank of Saddle Peak (SP). Northeast Baldy Mountain (NB) collecting locality is on the ridge crest (arrow) with Baldy and Bridger Mountains just to the south. Long ridge crest here is made up of thin-bedded Lodgepole Limestone generally dipping to the east. Two small Waulsortian bioherms in the lower Lodgepole (white patches labelled with W's) can be seen on the west-facing scarp face just north of Northeast Baldy. See Skipp and McMannis (1971).

Text-Figure 5. View of the west face of Bandbox Mountain (BD) in the northern Little Belt Mountains showing elongate Waulsortian bioherm or bank (white cliff) just below skyline. Original *Koryschisma* block found loose in talus chute at base of Lodgepole Limestone measured section at lower arrow; lithology was traced up to beds at 170–175 ft (52–53 m) above base where additional specimens collected in chute and on ridge crest (two upper arrows).

Text-Figure 6. View of the Upper Devonian and Lower Mississippian section on the north face of Crown Mountain (CM) in the Lewis and Clark Mountains of northwestern Montana. Cliffed part of the exposure (the mountain's "crown") is the lower Allan Mountain Limestone bearing *Tanaoblastus allanensis*, n. sp.

One of the major problems of using acetic acid, its slow reaction with the limestone matrix, was partly overcome either by heating the acid on a hotplate to a temperature between 110° and 130° F or by starting with hot water at this temperature. This elevated temperature increased the rate of reaction of acetic acid to about two-thirds the rate of cold, dilute hydrochloric acid, but still yielded excellent preservation.

At some of the Lodgepole blastoid localities, there is a marked contrast between the type of preservation developed during natural weathering and that achieved by extraction using heated acetic acid. The best example of this condition is found at the Standard Creek Section (ST) on the slopes of Cave Mountain in the Gravelly Range of southwestern Montana (see Text-Fig. 1), where nearly 500 specimens of *Tanaoblastus* have been collected. Natural weathering of these blastoids has produced a rather coarse, granular, pitted surface on the exposed portions of nearly all these specimens that has destroyed much of the finer detail of the ambulacra, oral and anal regions, and calyx ornamentation. If these specimens are extracted from the surrounding limestone matrix by using heated acetic acid, in most specimens the unweathered parts are somewhat better preserved than the weathered parts. In about 20% of the specimens, there is an extreme contrast in preservation (see Plate 1, Fig. 1). In these specimens, the unweathered parts of the theca show excellent preservation and remarkably fine detail, especially of the ambulacral areas and thecal ornament, in contrast to the naturally weathered parts. The preserved detail on these acid-extracted, silicified specimens appears to be equal to that found on the best-preserved calcitic blastoids from other localities.

It is not clear why this contrast in preservation is present, or why it occurs only at certain Lodgepole localities. This same difference in preservation was also found at the Dry Hollow (DH) and Milligan Can-

yon East (MC[E]) Sections (see Text-Fig. 1), where some of the specimens of *Orophocrinus, Strongyloblastus*, and *Metablastus* show the same contrast (see Plate 1, Figs. 2–5). However, at the nearby London Hills Section (LH), only 10 miles (16 km) to the west, where specimens of *Tanaoblastus, Strongyloblastus*, and *Metablastus* have been found, the fossils are well silicified but the preservation is rather poor on all of the specimens no matter if weathered or extracted with hydrochloric acid or heated acetic acid. This difference in preservation appears to be primarily controlled by the nature and degree of silicification of the blastoids themselves (including the hollow interiors), but apparently is also influenced by the degree of weathering and type of natural exposure, and by the nature of the surrounding limestone matrix. Etching by lichens may be another factor degrading the quality of silicified specimens during natural weathering.

One locality in the middle Lodgepole has weakly silicified blastoid specimens with delicate appendages (brachioles and stem segments) still attached. Many of these specimens on limestone slabs were uncovered and cleaned using an S. S. White air abrasive unit with dolomite powder. Two specimens from this locality and a few silicified or unsilicified specimens from other localities were ground down using abrasives on a glass plate to obtain information on the summit and internal structures of the theca.

PREVIOUS STUDIES OF MADISON BLASTOIDS

Only three short taxonomic articles describing a total of three blastoid species from the Early Mississippian of the northern U.S. Rocky Mountains have been published in the last 120 years (Meek, 1873; Hambach, 1903; Clark, 1917). However, during this period, at least five other authors have reported the presence of unstudied blastoids in faunal lists from the Lower Mississippian formations in this region (White, 1879; Laudon and Severson, 1953; Mudge, Sando, and Dutro, 1962; Sando and Dutro, 1980), indicating that blastoids may be a more common element in the faunas than usually thought. One of these occurrences from the Sappington Member of the Three Forks Formation (Gutschick, Suttner, and Switek, 1962, p. 82), now considered Late Devonian, was studied in detail by the present authors (Sprinkle and Gutschick, 1966, 1967). Other previously reported Mississippian blastoid occurrences appear to be from the overlying Madison Group (and its equivalents).

Meek (1873, p. 470) was the first author to describe a blastoid, *Pentremites bradleyi*, from the "Madison Formation" of the northern Rocky Mountains. Hambach (1903) restudied Meek's three specimens deposited in the Smithsonian Institution and, in addition to redescribing two of the specimens under the original name, designated the third specimen as a new species in a different genus, *Cribroblastus schucherti*. Clark (1917, pp. 361–373) reviewed all the previous reports of blastoids in the northern Rockies, and described a new species from the "Madison limestone" under the name *Schizoblastus haynesi*. Unfortunately, no summit (oral) views of either of his figured type specimens were presented in this paper, and this has resulted in some subsequent confusion about their correct generic assignment. Clark mentioned (p. 362) that White (1879, p. 80) had reported the occurrence of *Schizoblastus lotoblastus* from the Teton Range in western Wyoming, and Clark also described (pp. 369–370) a poorly preserved blastoid from "Old Baldy, near Virginia City, Montana" (Gravelly Range) as *Pentremites conoideus*. No additional blastoid material was mentioned until Laudon and Severson (1953, fig. 2a) listed *Cryptoblastus* in a measured section of the Lodgepole Limestone (lower Madison Group) from the Bridger Mountains of southwest Montana. Mudge, Sando, and Dutro (1962, p. 2017) listed *Pentremites* sp. in a faunal list

from the Castle Reef Dolomite (an upper Madison equivalent) in the Sun River Canyon area of northwestern Montana. Sando and Dutro (1980, p. 42) listed *Cryptoblastus* sp. in a faunal list for the lower Lodgepole Limestone from the northern Gravelly Range of southwestern Montana, probably the same Baldy Mountain locality as given above by Clark.

During the past fifty years, there has been much confusion about the true generic assignment of Clark's and Hambach's described species. In 1937, Fritz and Cline reported the occurrence of small globular blastoids from the Mississippian Banff Shale or Rundle Limestone on Mt. Coleman in western Alberta; additional blastoids from the Banff in the Sunwapta Pass area were reported by Laudon, Parks, and Spreng (1952). Fritz and Cline compared their Canadian material to Clark's Montana specimens, and kept his specific name, but reassigned both groups of specimens to the genus *Mesoblastus* on the basis of their material (Fritz and Cline, 1937, p. 309). Unfortunately, they did not restudy Clark's original types, but relied on the incomplete set of photographs in his 1917 paper. Peck (1938, p. 57), in a study of the blastoid fauna of the Chouteau Formation in Missouri, remarked that Clark's Montana specimens closely resembled some of his Missouri specimens of Kinderhookian age then assigned to the genus *Cryptoblastus*, but declined to consider the Montana specimens any further because of Fritz and Cline's assignment of these specimens to *Mesoblastus* during the previous year. In 1961, Fay restudied both Peck's *Cryptoblastus* material from the Chouteau of Missouri and Clark's holotype from Montana (MCZ 347) and assigned both forms to his new genus *Tanaoblastus* along with a single lower Burlington Limestone species from Missouri (Fay, 1961, pp. 101–104). However, *Tanaoblastus* and *Cryptoblastus* appear to be very closely related and there is still some question as to the correct assignment of certain species now assigned to each of these genera.

Galloway and Kaska (1957) reviewed the genus *Pentremites* and assigned Meek's *P. bradleyi* to their *Pentremites sulcatus* group (p. 74) because of its described slightly concave ambulacra, but they did not restudy the type specimens deposited in the Smithsonian Institution. Macurda (1962, pp. 1372–1373; 1978, p. 1293) in a discussion of Hambach's form "*Schizoblastus*" *schucherti*, mentioned that the original suite of specimens came from Idaho near the Montana border, and in 1978 provisionally assigned these forms to *Cribroblastus cornutus*. Luke and Moyle (1976) reported a similar occurrence of this species in the Brazer Formation of northern Utah,

→

PLATE 1

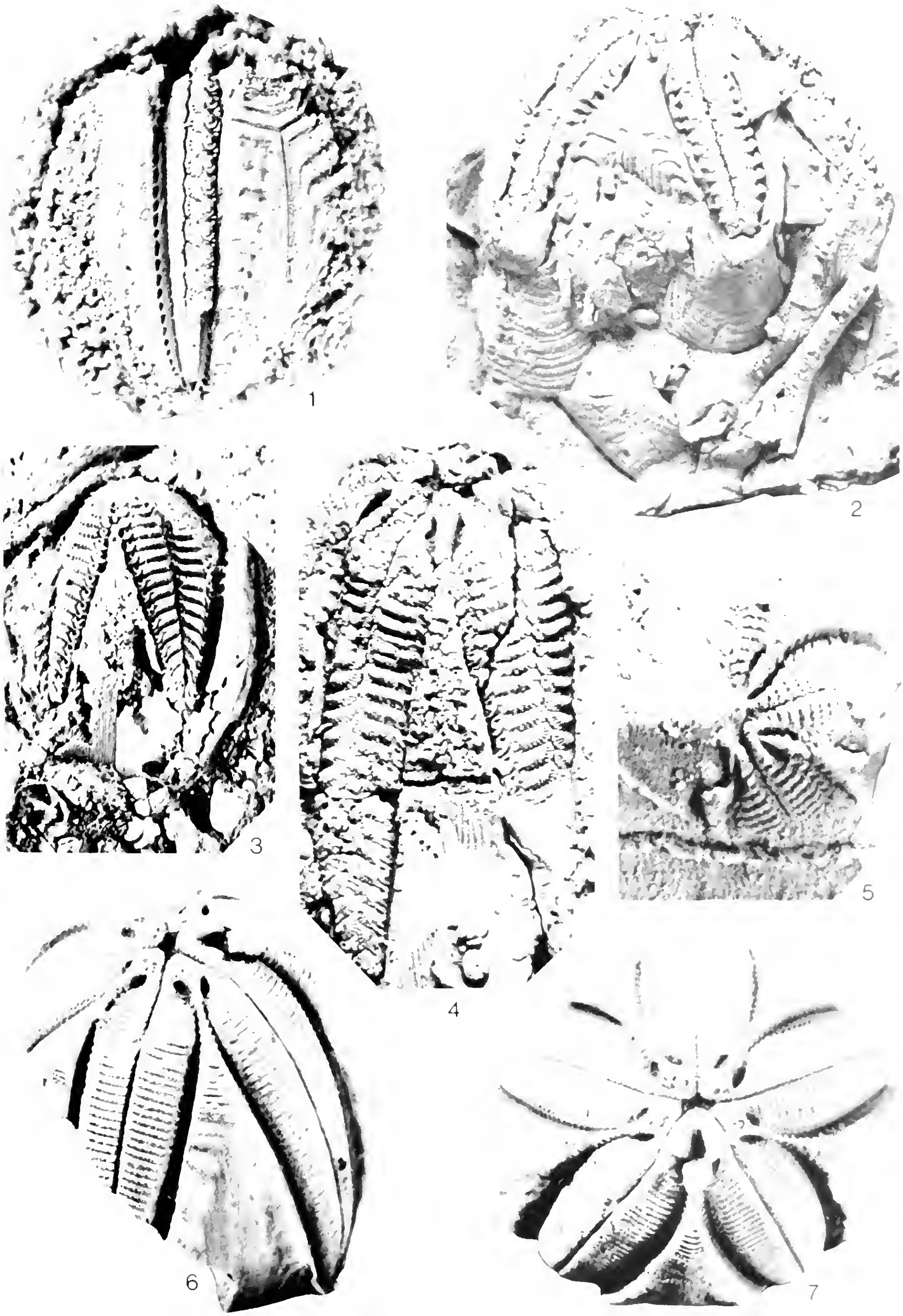
Figure 1. *Tanaoblastus haynesi* (Clark), lower Paine Member, lower Lodgepole Limestone, Standard Creek, southwestern Montana; side view of small theca MCZ 1024 showing contrast between coarse surface produced by natural weathering (around edges) and excellent preservation of ambulacral features and plate ornament formed by acetic acid etching (in center), ×12.

Figure 2. *Orophocrinus macurdai* Sprinkle and Gutschick, n. sp., lower Paine Member, lower Lodgepole Limestone, Dry Hollow, southwestern Montana; B-side view of partly-etched paratype MCZ 823 in slab; note excellent preservation of ambulacra, spiracular slits, and radial and deltoid ornament, ×6.3.

Figure 3. *Strongyloblastus laudoni* Sprinkle and Gutschick, n. sp., upper Paine Member, middle Lodgepole Limestone, Northeast Baldy Mountain, southwestern Montana; side view of paratype MCZ 878 in slab showing well-preserved ambulacra and growth lines on radials, ×6.

Figures 4–5. *Strongyloblastus breimeri* Sprinkle and Gutschick, n. sp., lower Paine Member, lower Lodgepole Limestone, Dry Hollow and Milligan Canyon East, southwestern Montana; 4, oblique EA-side view of paratype MCZ 854; note well-preserved ambulacra, spiracles, and growth lines on radials, ×7.5; 5, top view of paratype MCZ 849 still partly embedded in matrix showing C-spiracle cut off from rest of anispiracle by thin epideltoid septum (compare with 7 below), ×9.

Figures 6–7. *Strongyloblastus petalus* Fay, Banff Formation, western Canada; oblique DE-side and top views of partly-complete [illegible] theca UMR 6967 (Spreng Collection); note excellent preservation, wide ambulacra with curved food grooves near mouth, [illegible] deltoids, regular spiracles separated by raised deltoid septa, and very large horseshoe-shaped epideltoid that connects [illegible] with raised hypodeltoid cutting off C-spiracle from central anus but leaving D-spiracle barely connected, ×3.7.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a unit that has produced several other Late Mississippian blastoids (see Peck, 1930).

LODGEPOLE AND ALLAN MOUNTAIN BLASTOID FAUNAS

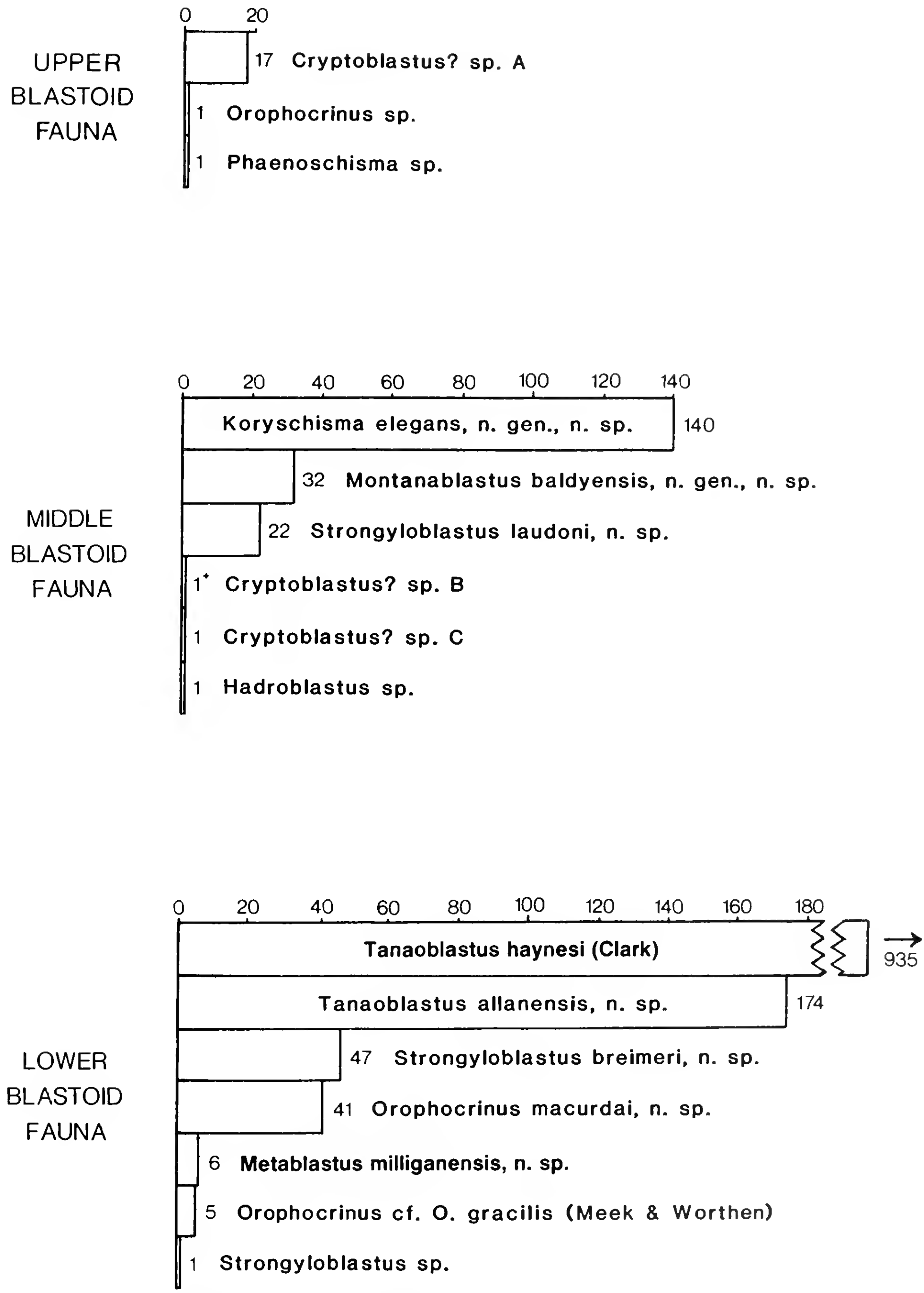
Lower Lodgepole Blastoid Fauna

The lower Lodgepole blastoid fauna is the most abundant, widespread, and diverse fauna known from the Rocky Mountains. This fauna has been found in the fossiliferous cherty beds between 5 and 75 ft (1.5–23 m) above the base of the Lodgepole and Allan Mountain Limestones (Text-Fig. 2) at 31 sections in southwestern, west-central, and northwestern Montana and in extreme southeastern Idaho (Text-Fig. 1). This blastoid fauna consists of four genera (*Tanaoblastus*, *Orophocrinus*, *Strongyloblastus*, and *Metablastus*) and seven species. About 1,220 specimens of this fauna were collected during four summers of field work (1963–66) and several later visits. This blastoid fauna is characterized by the dominance of the small globular genus *Tanaoblastus* overshadowing the other members of the fauna over its entire range. *Tanaoblastus* is by far the most abundant blastoid in the fauna, with 1,109 specimens (91% of the entire fauna) vs. 48 specimens (4%) for *Strongyloblastus*, 46 specimens (3.8%) for *Orophocrinus*, and six specimens (0.5%) for *Metablastus* (Text-Fig. 7). *Tanaoblastus* is also by far the most widespread, highest- and lowest-ranging form in the zone, and usually the dominant blastoid at any particular section. However, at a small number of Lodgepole sections just west of Three Forks in southwestern Montana, *Tanaoblastus* is a minor element and its place is taken by *Orophocrinus* and *Strongyloblastus*, with *Metablastus* also appearing rarely at these sections (Text-Fig. 8).

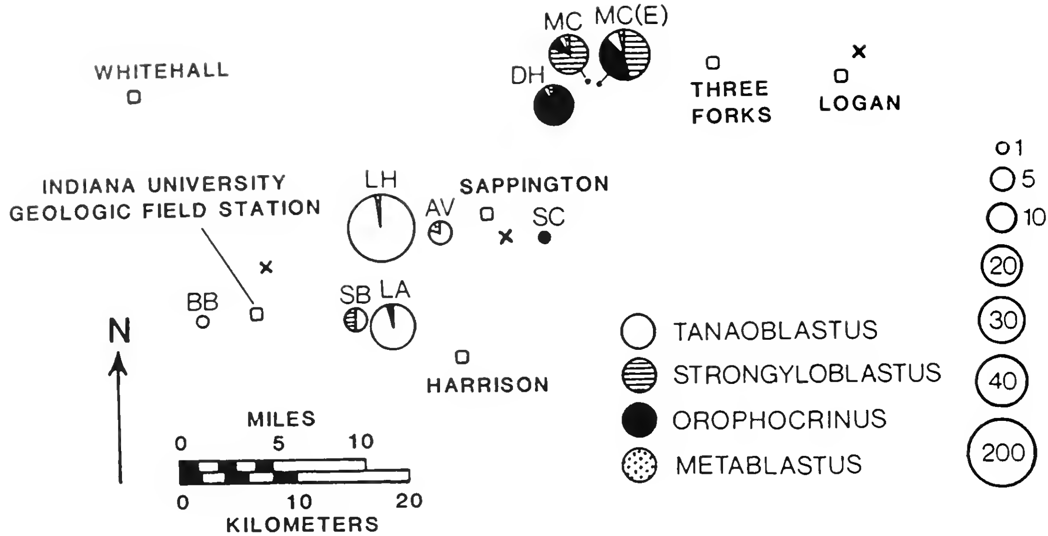
Middle Lodgepole Blastoid Fauna

Blastoids have been found between 110 and 200 ft (34–61 m) above the base of the Lodgepole at four scattered localities in southwestern and central Montana. The five genera and six species from these levels have been grouped together and collectively designated as the middle Lodgepole blastoid fauna (Text-Fig. 7). However, no more than three of these genera apparently occur together at any one section, and the four known occurrences may be at significantly different stratigraphic levels. One large group of specimens (about 50) has been found at three sections in the Bridger Range in southwestern Montana. Four specimens were collected in the early 1950s by Lowell R. Laudon from 110 to 125 ft (34–38 m) above the base of the Lodgepole from the Fairy Lake and Cottonwood Canyon Sections; these were listed as "*Cryptoblastus*" at this level in a stratigraphic section (Laudon and Severson, 1953, p. 509). At Laudon's suggestion, we visited a long exposure on the crest of the Bridger Range just north of Baldy Mountain (the Northeast Baldy Section [NB] in Text-Figs. 1 and 4) during the summer of 1966, and collected over 45 additional specimens, some partly silicified but many still calcitic with attached stems and brachioles. Three genera are present: *Strongyloblastus*, *Montanablastus*, n. gen., and *Cryptoblastus*? Unfortunately, we were not able to determine the exact position of this horizon because of faulting between the NB blastoid locality and the base of the Lodgepole about half a mile (0.8 km) to the south, but it is thought to be about 150 to 175 ft (46–53 m) above the base of the Lodgepole.

A second blastoid locality in the middle Lodgepole was discovered in August 1966 at Bandbox Mountain (BD) (Text-Figs. 1 and 5) in the northern Little Belt Mountains of west-central Montana. A large float block bearing a single exposed silicified blastoid was discovered in a talus chute at the base of the Lodgepole section and traced back up to a series of massive black beds between 170 and 175 ft (52–53 m) above the base. However, only a few additional specimens could be collected in place, and instead the talus block, weighing about 30 lb (13.6 kg), was carried out intact and shipped back to Harvard Uni-



Text-Figure 7. Bar graph showing the composition of the three blastoid faunas in the Lodgepole and Allan Mountain Limestones. Note abundance and diversity of these faunas and dominance of the lower blastoid fauna by *Tanaoblastus haynesi*; at true scale, its bar would extend nearly five times further to the right.



Text-Figure 8. Detailed map of the west-central part of the study area showing the abundance of different blastoid genera in the lower Lodgepole blastoid fauna. Note that *Tanaoblastus* is the dominant genus at many sections, but is replaced as most common by *Orophocrinus* and *Strongyloblastus* at three sections just west of Three Forks.

versity, in the hope that additional blastoids could be recovered by acid etching. The results proved to be well worth the effort (see Text-Fig. 9 and Plate 2). More than 35 complete and fragmentary specimens and several hundred separate plates of the new fissiculate genus *Koryschisma* were recovered from this block in addition to four plates and fragments of a small globular spiraculate blastoid, here designated as *Cryptoblastus*? sp. B. *Koryschisma* is the first fissiculate blastoid of the Phaenoschismatidae to be discovered in the northern Rockies, and because of the excellent preservation of these silicified specimens and separate plates, is probably the most completely known genus of the entire family. Two additional blastoid specimens, apparently from the middle Lodgepole, were recently collected by the late James Welch near Ant Park in the central Little Belt Mountains (see Plate 5, Fig. 9).

The last member of the middle Lodgepole blastoid fauna is a single specimen of *Hadroblastus* sp. from the Standard Creek Section (ST) in extreme southwestern Montana. This specimen was found on a [illegible] of crinoids on the talus slope above the lower cliff on Cave Mountain where *Tanaoblastus* is abundant. The top of the exposed Lodgepole beds at this locality is about 250 ft (76 m) above the base, so that this single specimen could have come from anywhere between 100 and 250 ft (30–76 m) above the base. The single calcite specimen has the proximal stem and a few of the brachioles preserved and was further uncovered using an air abrasive unit.

Upper Lodgepole Blastoid Fauna

The 19 specimens of the upper Lodgepole blastoid fauna are only known from the Bridger Range in southwestern Montana. The three genera and species in this fauna are very unequally represented because two of the genera are known from only a single specimen apiece. Fifteen specimens (mostly fragmentary) of *Cryptoblastus*? sp. A were found in a single bed at 655 ft (200 m) above the base of the Lodgepole along the sloping ridge east of the Sacagawea Peak Section (SA) (Text-Fig. 3) in the northern Bridgers; two additional specimens thought to represent this same form were found on a ripple-marked

limestone surface exposed in place in a small saddle near the Baldy Mountain Section (BY) (Text-Fig. 4) in the southern Bridgers, along with a single specimen of *Orophocrinus* sp. This bed appears to be near the top of the Lodgepole (probably in the upper 200 ft or 61 m), but its exact position could not be determined. A single specimen of *Phaenoschisma*? sp. was found in the float on the north flank of Saddle Peak in the southern Bridgers; it also appears to have come from the upper 200 ft (61 m) of the Lodgepole. The Lodgepole Limestone is about 800 ft (244 m) thick in the southern Bridgers, so that all of the specimens in the upper Lodgepole blastoid fauna probably came from beds between 600 and 800 ft (183–244 m) above the base of the formation (see Text-Fig. 2).

Both the middle and upper Lodgepole blastoid faunas are less well known than the abundant and widespread lower Lodgepole blastoid fauna, implying that these younger faunas could be considerably more diverse than is presently known. We found no blastoids between 200 and 600 ft (61–183 m) above the base of the formation, although fossiliferous and apparently favorable beds are present at several sections. Additional blastoid genera and localities will probably be found in the upper part of the Lodgepole in western Montana and adjacent areas as more field work is done on these units.

OCCURRENCE AND DISTRIBUTION

Of the three blastoid faunas now known from the Lodgepole and Allan Mountain Limestones in western Montana, only the lower fauna is sufficiently widespread and abundant to permit an analysis of its distribution pattern. Blastoids in the lower fauna have been collected at 31 of the 57 Lodgepole and Allan Mountain sections in western Montana studied by the authors during 1964–66 (Text-Fig. 1). A dividing line running through western Montana (see Text-Fig. 1) separates an area to the west and southwest where blastoids are consistently absent from a region to the east and northeast where blastoids are present at about 75% of the lower Lodgepole and Allan Mountain Limestone sections studied. This distribution trend appears to correspond to a lithologic change in the lower Lodgepole beds between 5 and 75 ft (1.5–23 m) where the lower blastoid fauna occurs. Three major factors are necessary in order for blastoids to be found at any given section: (1) good exposure, (2) the presence of a normal lower Lodgepole fauna, and (3) the occurrence of chert with corresponding silicification of the fossils. Good exposures of the lower Madison are present at many localities in western Montana, both east and west of this dividing line, so that exposure is generally not a factor. The characteristic fauna typically found in association with the blastoids disappears toward the west, probably because of a gradual facies change in the lower Lodgepole beds. The amount of chert present in these beds and the corresponding degree of silicification of the fauna also diminishes to the west, and again appears to be controlled by the source and amount of silica present. The disappearance of both the

Text-Figure 9. Partly etched, original block from the middle Lodgepole Limestone at Bandbox Mountain (BD) showing the abundance of *Koryschisma* thecae, plates, flanged columnals, and brachiole fragments in some beds. Complete specimens include (from left edge): unnumbered cracked theca, MCZ 925 (above), MCZ 921 covered with debris, large holotype MCZ 915, the base of which was the only identifiable blastoid part originally exposed, broken MCZ 927 (above), and MCZ 926. Millimeter and centimeter scale at lower right.

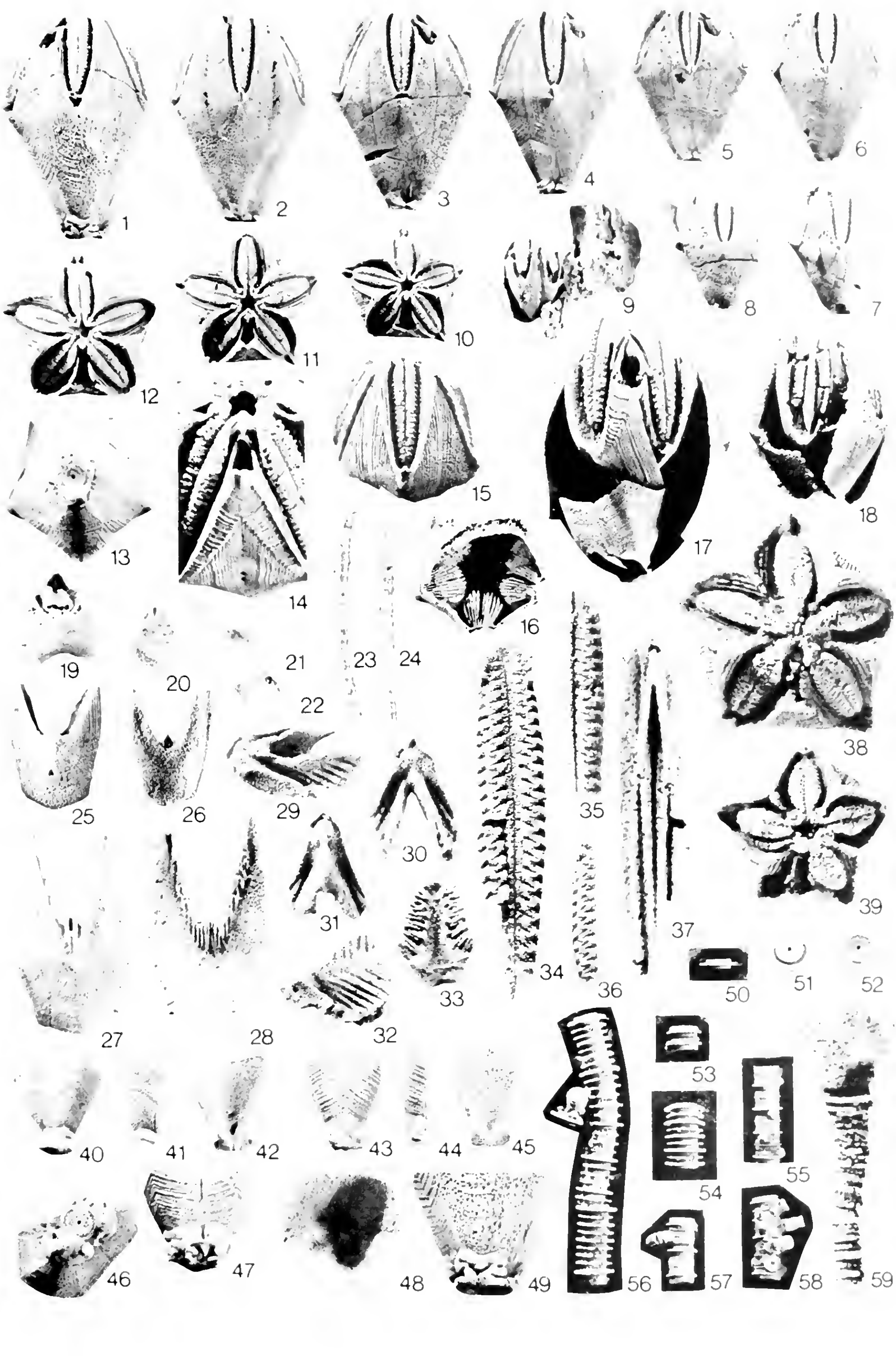
fauna and silicification are probably the result of increasing water depth to the west.

In the eastern part of the area, the beds between 5 and 75 ft (1.5–23 m) are composed of massive-bedded, fine-grained, micritic limestones that are cherty and contain an abundant silicified fauna, including common blastoids, especially in the lower part of the section. To the west, the upper boundary of these fossiliferous, cherty beds appears to gradually migrate down-section, and they are replaced by rhythmically interbedded, dark, micritic limestones and lighter dolomitic shales lacking both fossils and chert. Near the boundary line between the two areas, the chert and then the fossils (including the blastoids) are lost from the lower part of the section. West of the dividing line, these rhythmically banded limestone-shale alternations begin at the top of the resistant basal ledge in the Paine Member only 3 to 5 ft (0.9–1.5 m) above the base, and fossils and chert are absent above this level. The cherty, fossiliferous beds to the east apparently represent upramp, shallow-water deposition, in contrast to the rhythmic, parallel-interbedded dark limestones and dolomitic shales devoid of fossils and chert to the west that appear to represent deeper water deposition well below wave base (Text-Fig. 10). Apparently subsidence was more rapid in the western part of the area above the basal Paine unit than to the east where the shallow-water blastoids and other fossils commonly occur.

→

PLATE 2

Figures 1–59. *Koryschisma elegans* Sprinkle and Gutschick, n. gen., n. sp., upper Paine Member, middle Lodgepole Limestone, Bandbox Mountain, northern Little Belt Mountains, west-central Montana. 1, 12–13, 49, C-side, top, bottom, and enlarged basal deposits of holotype MCZ 915 showing large size, missing hypodeltoid, medium growth lines, and very large secondary deposits at stem facet, ×2 and ×3(49); 2, 11, 14, C-side, top, and enlarged oblique summit views of large paratype MCZ 916; note growth lines and raised hypodeltoid still in place, ×2 and ×4(14); 3, D-side view of large paratype MCZ 917 showing several cracks through theca, ×2; 4, D-side view of medium paratype MCZ 918; note fine growth lines and missing hypodeltoid, ×2; 5, 10, D-side and top views of medium paratype MCZ 919 showing lower L/W ratio than 6, missing hypodeltoid, and large lips at RR origins, ×2; 6, A-side view of medium paratype MCZ 920; note elongate shape and fine growth lines, ×2; 7, C-side view of medium paratype MCZ 921 with tip of BB broken off, ×2; 8, B-side view of small paratype MCZ 922 stuck to a radial plate, ×2; 9, C-side view of small paratype MCZ 923 which is partly disarticulated and stuck to a piece of silicified matrix, ×2; 15–16, E-side and bottom views of broken paratype MCZ 924 showing relatively coarse growth lines, hydrospire slits in ambulacral sinus wall, and well-preserved hydrospires in thecal cavity, ×2.5 and ×2; 17, CD-side view of large crushed paratype MCZ 928; note one-piece epideltoid and development of growth lines on D radial, ×3; 18, side view of medium paratype MCZ 927 showing side plates lying beside partly-exposed lancet, ×3; 19, broken radial plate with ambulacrum (paratype MCZ 956); note large radial lip, cross-sectional shape of ambulacrum, and trace of hydrospires, ×3; 20–22, exterior, left edge, and adoral views of three hypodeltoids (paratypes MCZ 952, 951, and 953) showing adoral projection and faint growth lines, ×6; 23–24, two brachiole segments (paratypes MCZ 958 and 959); note brachiolar plates and trace of cover plates (at left), ×6; 25–26, small paratype radial MCZ 954 showing shape and plate thickness, ×6; 27–28, large paratype radial MCZ 957; note growth lines, much longer ambulacral sinus, and trace of hydrospire folds on interior, ×3; 29–30, oblique edge and exterior views of paratype epideltoids MCZ 950 and 949 showing limbs infolded into hydrospires and right limb extending higher on plate than left limb, ×6; 31–33, exterior, edge, and aboral views of paratype deltoids MCZ 948, 946, and 947; note serrated crest, curved RD suture, and numerous hydrospire folds, ×6; 34, 37, exterior and interior of nearly complete paratype ambulacrum MCZ 942 showing lancet exposure, side plates with lateral spines adorally, and deep groove beneath lancet, ×6; 35, partial ambulacrum (paratype MCZ 944) with exposed lancet and right set of side plates, ×6; 36, partial side plate set (paratype MCZ 945) from left side of ambulacrum, ×6; 38, top view of paratype theca UMMP 60694 (Macurda Collection, no. 16 in growth series) showing tiny oral cover plates in place over mouth and adoral ambulacra, ×4; 39, top view of abnormal paratype theca UMMP 60688 (Macurda Collection, no. 10 in growth series); note two ambulacra combined together in E ray and no ambulacrum (or food groove) in D ray, ×3; 40–42, exterior, edge, and interior views of paratype BD basal MCZ 940 showing shape, growth lines, and oblique depression just above stem facet (42), ×3; 43–45, exterior, edge, and interior views of paratype azygous AB basal MCZ 941; note narrower shape and slightly coarser growth lines, ×3; 46–48, aboral, side, and adoral views of large paratype basal set MCZ 939 showing shape, growth lines, and very heavy secondary deposits forming stem facet, ×3; 50, side view of single paratype columnal MCZ 936 with flange, ×2; 51–52, top views of two paratype columnals MCZ 934 and 935; note central lumen, tiny crenulae, and different-sized flanges, ×2; 53, side view of two flanged columnals (paratype MCZ 937), ×2; 54, side view of short proximal stem segment (paratype MCZ 930) showing closely-spaced alternating columnals, ×2; 55, side view of distal stem segment (paratype MCZ 933); note widely-spaced alternating columnals and cirri branching off between flanges, ×2; 56, side view of longest preserved stem segment (paratype MCZ 931) showing alternation of columnal types in proximal stem, ×2; 57, side view of distal stem segment (paratype MCZ 932); note somewhat overgrown columnals and one large cirrus, ×2; 58, side view of distalmost stem segment (paratype MCZ 938) with numerous cirri or rootlets branching off mostly from right side, ×2; 59, side view of very small basal set and attached proximal stem (paratype MCZ 961), ×6.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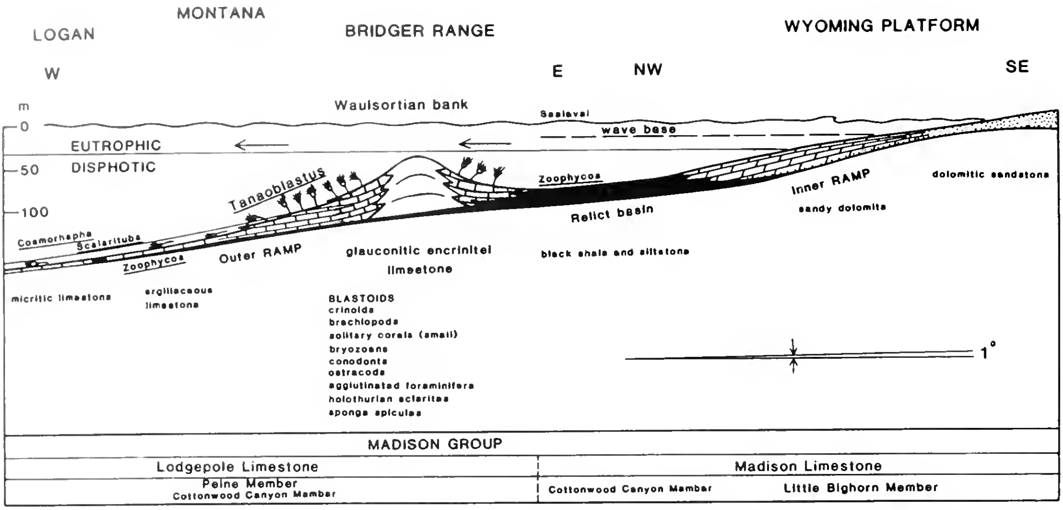


Text-Figure 10. Transect across western Montana showing the paleoecologic setting for the lower Lodgepole blastoid fauna during the *Siphonodella crenulata* Zone. Although they were uncommon and widely spaced in the outer ramp, a Waulsortian bioherm is shown in this cross section growing upward toward the surface with blastoids living on its flanks (after Sandberg and Gutschick, 1983).

In the eastern part of the area where blastoids are relatively abundant, the small globular genus *Tanaoblastus* is clearly dominant in the lower Lodgepole and Allan Mountain blastoid fauna. It is present at nearly every lower Lodgepole and Allan Mountain section where blastoids have been found. At most sections, *Tanaoblastus* is either the only form present or the dominant form, and is represented by a total of 1,109 specimens or about 88% of all the blastoids collected. Elongate ellipsoidal specimens of *Strongyloblastus*, conical and biconical specimens of the fissiculate *Orophocrinus*, plus biconical specimens of *Metablastus* also occur in this lower zone fauna, but are much less common and more restricted in their distribution. Specimens of these other genera are most common at a few sections in the central part of the study area in southwestern Montana (see Text-Fig. 8), primarily Dry Hollow, Milligan Canyon, Milligan Canyon East, and South Boulder. Several other Early or Middle Mississippian blastoid faunas, such as those from the Tournaisian of Belgium (Macurda, 1967), the Lake Valley Limestone of New Mexico (Fay, 1962c), and the Chouteau Limestone of Missouri and Iowa (Peck, 1938), are also dominated by a small globular spiraculate blastoid, whereas other conical, biconical, or ellipsoidal blastoid genera are less common (see Table 2).

AGE OF THE BLASTOID FAUNAS

The age and zonation of the Lodgepole Limestone, including the intervals containing the blastoid faunas, were discussed in Gutschick, Sandberg, and Sando (1980); Sandberg *et al.* (1983, pp. 707–711); and Sando and Bamber (1985). The lower Lodgepole blastoid fauna occurs in the basal 75 ft (23 m) of the Paine Member which was deposited about 4.5 to 6 million years after the Devonian-Mississippian boundary (middle Kinderhookian, early Tournaisian) using the time scale of Palmer (1983). This unit was deposited during the time interval of the Lower *Siphonodella crenulata* conodont zone, Pre-7 foram zone (Sando, Mamet, and Dutro, 1969), and IB coral zone (Sando and Bamber, 1985). The blastoids in the lower fauna (Table 2) correlate best with those in the

TABLE 2. COMPARISON OF THE LOWER LODGEPOLE AND ALLAN MOUNTAIN BLASTOID FAUNA IN MONTANA WITH OTHER EARLY AND MIDDLE MISSISSIPPIAN BLASTOID FAUNAS FROM WESTERN CANADA, NEW MEXICO, MISSOURI (2 UNITS), AND BELGIUM. NOTE THAT ALL OF THESE FAUNAS HAVE A SMALL GLOBULAR, SPIRACULATE BLASTOID, USUALLY AS THE DOMINANT FORM.

Fauna	Small globular spiraculate	Large ellipsoidal spiraculate	Biconical spiraculate	Conical fissiculate	Other fissiculates
Lower Lodgepole and Allan Mountain Lmst., Montana (this study)	*Tanaoblastus* 1109	*Strongyloblastus* 48	*Metablastus* 6	*Orophocrinus* 46	—
Banff Formation, Alberta & British Col. (Fritz & Cline, 1937)	*Cryptoblastus*	*Strongyloblastus*	—	—	—
Lake Valley Limestone, New Mexico (Fay, 1962c)	*Monadoblastus*	—	—	*Phaenoschisma*	*Hadroblastus*, *Koryschisma*
Chouteau Formation, Missouri (Peck, 1938; Macurda, 1964)	*Tanaoblastus*	—	—	*Phaenoschisma*	*Hadroblastus*
Lower Burlington Limestone, Missouri (Sprinkle, pers. coll.)	*Globoblastus*, *Poroblastus*	"*Pentremites*"	*Dentiblastus*	*Phaenoschisma*	*Orophocrinus*, *Hadroblastus*
Tournaisian of Tournai, Belgium (Macurda, 1967)	*Mesoblastus* 200	—	—	*Orophocrinus*, *Katoblastus* 6 & 10	*Phaenoblastus*, *Katoblastus* 100 & 10

Chouteau Limestone of Missouri (see Peck, 1938) and those of the type-Tournaisian of Belgium (see Macurda, 1967). The middle Lodgepole blastoid fauna occurs between 110 and 200 ft (34–61 m) up in the Paine Member which dates about 6 to 7.5 million years after the Devonian-Mississippian boundary (late Kinderhookian, early Tournaisian) during the time interval of the *Siphonodella isosticha*–upper *S. crenulata* conodont zone, Pre-7 foram zone, and IC coral zone (Sandberg *et al.*, 1983). The middle Lodgepole blastoid fauna with its two new genera does not correlate well with blastoid faunas in other areas. The upper Lodgepole blastoid fauna occurs in the top 200 ft (61 m) of the overlying Woodhurst Member which was deposited 9–10 million years after the Devonian-Mississippian boundary (early Osagean, middle Tournaisian) during the time interval of the Lower *Gnathodus typicus* conodont zone, foram zone 7, and lower IIB coral zone (Sandberg *et al.*, 1983). The three blastoids in the upper Lodgepole fauna resemble those in the Osagean lower Burlington Limestone in Missouri.

PALEOGEOGRAPHY AND PALEOECOLOGY

A generalized regional paleogeographic pattern has evolved for the Early Mississippian history of western Montana (Holland, 1952; Wilson, 1969; Rose, 1976; Sando, 1976; Haines, 1977; Smith, 1977, 1982; Roberts, 1979; Gutschick, Sandberg, and Sando, 1980; Lane, 1982; Gutschick and Sandberg, 1983) that can provide the environmental setting for Lodgepole blastoids of this study (Text-Figs. 1 and 10). Montana in Early Mississippian time was a broad carbonate marine shelf covered by

the Madison Sea. An east-west unstable Central Montana Trough (Big Snowy and Crazy Mountains Troughs) separated two stable platforms, the Wyoming Shelf to the southeast and the Alberta Shelf to the northeast on the boundary with Saskatchewan and Alberta (Wilson, 1969; Smith, 1982). Broad, gently sloping, carbonate ramps of the drowned homoclinal type (Read, 1985) extended from the platforms into deeper water of the Central Montana Trough and westward towards the north-south miogeosyncline in western Montana (Text-Fig. 10). Drowning was in large part caused by sea level changes, including a major regression at the Devonian-Mississippian boundary, followed by a major transgression during Lodgepole deposition (*S. crenulata* and *G. typicus* conodont zones). Rhythms (cycles) of sedimentation in the Lodgepole and Allan Mountain Limestones (Wilson, 1969; Smith, 1972; Haines, 1977) may reflect minor transgressive-regressive fluctuations and subsidence.

Waulsortian-facies carbonate mounds (Text-Fig. 10) have been recognized downramp at Swimming Woman Canyon in the Big Snowy Mountains (Cotter, 1965, 1966), in the Bridger Range (Stone, 1972; see Text-Fig. 4), at Belt Creek Canyon (Wilson, 1969) and at Bandbox Mountain (Sandberg and Klapper, 1967; see Text-Fig. 5) in the Little Belt Mountains, and at Lone Butte and Crown Mountain (Haines, 1977; see Text-Fig. 6) in the Lewis and Clark Range. The best paleolatitudinal position of Montana during the Early Carboniferous from paleomagnetic data is approximately 5° North (C. R. Scotese, personal communication 7/18/86). This places the carbonate setting of our blastoid localities in the tropical realm just north of the paleoequator. The resulting wind pattern may have produced some upwelling towards the Wyoming Shelf. However, Van der Voo (1988) places the Late Devonian paleoequator just north of the Montana study area, so that it would be in the southern hemisphere tropics.

A transect depicting the paleoecological setting for the Early Mississippian blastoids of this study is presented in Text-Figure 10, extending from the Wyoming Shelf through the Bridger Range and westward beyond Logan, Montana, towards the Antler Flysch Trough (Mamet, 1972; Armstrong and Mamet, 1977; Sandberg and Gutschick, 1983). The lower Lodgepole and Allan Mountain blastoid faunas occur with a diverse assemblage of marine invertebrates representing an outer shelf environment on a carbonate ramp below normal wave base. Generalized faunal lists for the intervals yielding the lower and middle Lodgepole blastoid faunas are presented in Table 3.

Several faunal groups have been extensively studied, including the agglutinated foraminifera (Gutschick, Weiner, and Young, 1961; Gutschick, 1964, fig. 5; Sandberg and Gutschick, 1984), corals (Sando and Bamber, 1985), brachiopods (Rodriguez and Gutschick, 1968, 1969), crinoids (Laudon and Severson, 1953), holothurian sclerites (Gutschick, Canis, and Brill, 1967), goniatites (Gordon, 1986), conodonts (Klapper, 1966; Sandberg and Gutschick, 1983), and trace fossils (Rodriguez and Gutschick, 1970).

Taphonomic observations were made from silicified blastoids collected from bedding surfaces and blocks in the lower blastoid fauna; thanatocoenoses were extracted from acid residues and studied on bedding slab surfaces in the middle blastoid fauna. Blastoids most commonly occur with crinoids (especially disarticulated stems and plates), fenestellid bryozoans, and small brachiopods. Blastoids are rarely found in beds containing abundant corals but do occur with occasional small solitary corals and recumbent branching auloporids.

The Lodgepole blastoids were probably medium-level rheophilic suspension feeders. Most blastoid thecae are fairly small (5–20 mm long), and even the most complete preserved stem is only 29 mm long, although the original length may have been

several times this figure. This would put these blastoids in the middle tier of suspension feeders below the top canopy of long-stemmed crinoids but above low-level epifaunal forms such as the fenestellid bryozoans and brachiopods (Ausich and Bottjer, 1985).

It is unusual to find complete blastoid specimens with appendages intact. Only two localities with Lodgepole blastoids out of 37 had complete blastoids with appendages. This suggests that most blastoids were not buried instantly at the time of death or distal detachment but lay exposed on the seafloor after death for several days or weeks before being buried, thus allowing the delicate appendages to become dissociated (Sprinkle and Gutschick, 1967). Many specimens were subsequently crushed during diagenesis, probably because they were filled with soft sediment susceptible to compaction. Only a few blastoid thecae show any evidence of postmortem disturbance by burrowers (see Plate 4, Fig. 26).

Blastoids were not found by us within any of the Waulsortian bioherms in the Lodgepole. Blastoids were found at two localities in beds below and adjacent to Waulsortian bioherms, and they are shown living on the flanks of these mounds in our paleoecological diagram (Text-Fig. 10). *Tanaoblastus* from the lower fauna occurs just below and in flank beds adjacent to a small white bioherm in the lower Paine Member at the Bridger Mountain Section (BG) in the southern Bridger Range. At Bandbox Mountain in the northern Little Belt Mountains, the middle blastoid fauna occurs in black, thick-bedded limestones about 10 ft (3 m) below the base of a large white bioherm or bank (see Text-Fig. 5).

The lack of complete articulated fossil animals within the Waulsortian mound core, e.g., stalked crinoids or blastoids, should not seem unusual. The mound structure on the inclined ramp has relatively steep flanks, ranging from 5° to 29° (Cotter, 1965; Smith, 1982) to as much as 40° (Laudon and Bowsher, 1941). Globular calyces can easily be transported by gravity and traction currents out and away from the bioherms. In the case of Mississippian crinoids associated with Waulsortian bioherms in the Sacramento Mountains, New Mexico, large numbers of calyces (prolific Lake Valley crinoid fauna) accumulated downslope as scree on the leeward side flank of the bioherms in a geopetal fashion (Laudon and Bowsher, 1941, 1949, personal communication).

Agglutinated foraminifera, particularly the abundance of elongated tubular hyperamminids in the Lodgepole, inhabited the outer shelf and slope environment (Sandberg and Gutschick, 1984); small solitary corals of genera typical of the lower Lodgepole are deeper-water types (Sando, 1980; Gutschick and Sandberg, 1983, fig. 7C; Sando and Bamber, 1985). Species of the conodont *Siphonodella* are associated with offshore deeper-water environments (pelagic nekton) (Dreesen, Sandberg, and Ziegler, 1986), and the trace fossils *Scalarituba* and *Cosmorhaphe* inhabit the slope in offshore deeper water (Gutschick and Sandberg, 1983, fig. 7F). Fenestellid bryozoans (Cuffey, 1985), brachiopods, and the conspicuous lack of calcareous algae in the blastoid facies are compatible with this general environmental pattern.

SYSTEMATIC PALEONTOLOGY

Class BLASTOIDEA Say, 1825
Order FISSICULATA Jaekel, 1918
Family PHAENOSCHISMATIDAE Etheridge and Carpenter, 1886
Genus KORYSCHISMA Sprinkle and Gutschick, new genus

Type Species. Koryschisma elegans Sprinkle and Gutschick, new species.

Diagnosis. Fissiculate blastoids with an obconical theca, pelvis longer than vault, radials and deltoids raised into crests above ambulacra; 10 partly exposed hydrospire fields, 3–9 hydrospire slits per field (number increasing with size), number of slits slightly reduced on anal side; two anal deltoids, epideltoid with long aboral limbs,

TABLE 3. LISTS OF FOSSILS FOUND IN THE LOWER LODGEPOLE BLASTOID FAUNA 5–75 FT (1.5–23 M) ABOVE THE BASE OF THE LODGEPOLE AND ALLAN MOUNTAIN LIMESTONES AND IN THE MIDDLE LODGEPOLE BLASTOID FAUNA 110–200 FT (34–61 M) ABOVE THE BASE OF THE LODGEPOLE LIMESTONE IN WESTERN MONTANA. LOWER FAUNA BASED PARTLY ON A FIELD CENSUS TAKEN FROM TALUS BLOCKS AT STANDARD CREEK IN 1966; MIDDLE FAUNA BASED PARTLY ON ACID RESIDUES FROM BANDBOX MOUNTAIN (IDENTIFIED BY FRANCIS ZIMMER) AND ANT PARK, AND A CENSUS OF SLAB SURFACES COLLECTED FROM NORTHEAST BALDY MOUNTAIN →

Fossil group	Lower blastoid fauna	Middle blastoid fauna
Protozoa		
Foraminiferida		
Textulariina	*Hyperammina rockfordensis*	*Hyperammina rockfordensis-H. kentuckyensis* transit.
	Pseudastrorhiza digitata	—
	P. 2 species	—
	Trepeilopsis glomospiroides	—
	Ammobaculites leptos	—
	—	*Rheophax calathus*
	—	*R. raymoorei*
	—	*Tolypammina* sp.
Fusulinina	*Septglomospiranella* sp.	—
	Septabrunsiina sp.	—
	Latiendothyra sp.	—
	—	*Chernyshinella* sp.
	—	*Paleospiroplectammina* sp.
	—	*Rectoseptaglomospiranella* sp.
Porifera	Siliceous spicules	Siliceous spicules
	—	Globular form with spicules
Coelenterata		
Anthozoa		
Rugosa	*Amplexus* sp.	*Amplexus* sp.
	Amplexizaphrentis sp.	*Amplexizaphrentis* sp.
	Amplexocarinia sp.	*Amplexocarinia* sp.
	Cyathaxonia tantilla	*Cyathaxonia tantilla*
	Cleistopora placenta	—
	Metriophyllum deminutivum	—
	Neaxon? sp.	—
	Palaeacis sp.	—
	—	*Sychnoelasma subcrassum*
	—	*Stelechophyllum microstylum*?
Tabulata	*Aulopora* sp.	*Aulopora* sp.
	Cladochonus sp.	—
	—	*Syringopora* sp.
Bryozoa		
Cystoporata	—	*Cystodictya* sp.
	—	*Fistulipora* sp.
	—	*Sulcoretepora*? sp.
	—	Unidentified Cystodictyonid
Cryptostomata	—	*Nicklesopora* sp.
	—	*Rhombopora* or *Rhabdomeson* sp.
Fenestrata	Several Fenestellids	6 genera of Fenestellids
	—	*Hemitrypa* sp.
	—	*Penniretepora* sp.
	—	*Ptylopora* sp.
	—	Unidentified Acanthocladid
	—	*Septopora* sp.

(*continued*) IN 1966 AND 1984–85. PUBLISHED SOURCES FOR INFORMATION ON PARTICULAR GROUPS LISTED BELOW INCLUDE: GUTSCHICK (1964), GUTSCHICK, WEINER, AND YOUNG (1961), AND MAMET AND SKIPP (1970), FORAMS; SANDO (1983) AND SANDO AND BAMBER (1985), CORALS; MCKINNEY (PERSONAL COMMUNICATION, 1987), MIDDLE FAUNA BRYOZOANS; RODRIGUEZ AND GUTSCHICK (1968, 1969), LOWER FAUNA BRACHIOPODS; GORDON (1986), LOWER FAUNA AMMONOIDS; RODRIGUEZ AND GUTSCHICK (1970), TRACE FOSSILS; LAUDON AND SEVERSON (1953), CRINOIDS; GUTSCHICK, CANIS, AND BRILL (1967), HOLOTHURIANS; AND SANDBERG *ET AL.* (1978), CONODONTS.

Fossil group	Lower blastoid fauna	Middle blastoid fauna
Brachiopoda		
Inarticulata	*Crania* sp. cf. *C. blairi*	—
Articulata		
Orthida	*Rhipidomella* sp.	—
Strophomenida	*Caenanoplia logani*?	*Caenanoplia logani*?
	—	*Buxtonia*? sp.
	Productina lodgepolensis	—
	Leptagonia analoga	*Leptagonia analoga*
Rhynchonellida	*Camarotoechia* sp.	*Camarotoechia metallica*
	—	*C. tuta*
	—	*C. inaequa*?
	Axiodeaneia platypleura	—
Spiriferida	*Cleiothyridina* sp.	*Cleiothyridina obmaxima*
	—	*C. glenparkensis*
	—	*C.* sp. cf. *C. incrassata*
	Crurithyris parva?	—
	Cyrtina burlingtonensis	—
	—	*Eumetria osagensis*?
	Hustedia texana	*Hustedia texana*
	Nucleospira obesa	—
	Plectospira? *problematica*	—
	—	*Prospira greenockensis*?
	—	*Punctospirifer solidirostris*
	—	*Reticularia cooperensis*?
	Spirifer sp.	*Spirifer missouriensis*
	—	*S. albapinensis*
Terebratulida	*Dielasma*? sp. cf. *D. utah*	*Dielasma* sp. cf. *D. utah*
Mollusca		
Gastropoda	*Platyceras* sp.	*Platyceras paralius*
	—	*P.* 3 sp.
	—	*Goniospira* sp.
	—	*Bellerophon* sp.
	Several other genera	At least 8 other genera
Bivalvia	—	*Palaeoneilo missouriensis*
	—	*Allorisma*? sp.
	—	*Leptodesma* sp.
	Unidentified small bivalves	—
Cephalopoda		
Nautiloidea	*Triboloceras digonum*	—
	—	1 orthoconic genus
Ammonoidea	*Imitoceras* sp.	1 or more goniatites
	Gattendorfia costata	—
	Pericyclus rockymontanus	—
	Rotopericyclus sp.	—
"Worms"	—	*Spirorbis nodulosus*
	Spirorbis sp.	*S.* sp.
	—	*Tentaculites* sp.

TABLE 3. CONTINUED.

Fossil group	Lower blastoid fauna	Middle blastoid fauna
Trace Fossils	*Cosmorhaphe* sp.	*Cosmorhaphe* sp.
	Scalarituba missouriensis	*Scalarituba missouriensis*
	—	*Zoophycos* sp.
	Horizontal burrows	Horizontal burrows
Arthropoda		
Trilobita	—	*Richterella snakedenensis?*
Ostracoda	Several genera	Several genera
Echinodermata		
Crinoidea		
Inadunata	*Amphelecrinus madisonensis*	*Amphelecrinus madisonensis*
	Linocrinus walsallensis	—
	Unidentified microcrinoids	—
Camerata	*Abactinocrinus rossei*	—
	Actinocrinites sp.	—
	—	*Cactocrinus arnoldi*
	Platycrinites bozemanensis	*Platycrinites bozemanensis*
	—	*Rhodocrinites douglassi*
Blastoidea		
Fissiculata	*Orophocrinus macurdai*	—
	O. sp. cf. *O. gracilis*	—
	—	*Koryschisma elegans*
	—	*Hadroblastus* sp.
Spiraculata	*Tanaoblastus haynesi*	—
	T. allanensis	—
	—	*Cryptoblastus?* sp. B
	—	*C.?* sp. C
	Strongyloblastus breimeri	*Strongyloblastus laudoni*
	S. sp.	—
	—	*Montanablastus baldyensis*
	Metablastus milliganensis	—
Asteroidea	—	Starfish arm
Ophiuroidea	—	2 unidentified genera
Edrioasteroidea	—	2 specimens of 1 genus
Echinoidea	—	*Archaeocidaris aliquantula*
Holothuroidea	*Achistrum coloculum*	—
	A. gamma	—
	Eocaudina columcanthus	—
	E. subhexagona	—
	E. marginata	—
	Microantyx botoni	—
	M. mudgei	—
	Rota campbelli	—
	R. martini	—
Conodonta	*Siphonodella crenulata*	*Siphonodella crenulata*
	—	*Siphonodella isosticha*
	Several other genera & species from Lower *crenulata* Zone	Several other genera & species from Upper *crenulata-isosticha* Zone
Vertebrata		
Osteichthyes	—	Brachyodont crushing tooth
Totals	67+ Genera	83+ Genera

hypodeltoid, pointed or hooded, having wide growth front on thecal surface; regular deltoids fairly small, either barely appearing on thecal surface with tiny external DR growth sector, or confined to ambulacral sinuses, radials strongly overlap deltoids near thecal surface but overlap gradually reverses deeper into sinuses; ambulacra moderately long, linear to lanceolate, extending out from mouth in shallow sinuses or down theca in relatively deep sinuses, lancet slightly exposed, side plates usually conceal about two-thirds of slits in sinus walls; brachioles small, ridged on sides; stem made up of flanged columnals, cirri and rootlets present distally for attachment of stem to substrate using recumbent rhizoid holdfast.

Occurrence. Early Mississippian (Late Kinderhookian = Tournaisian) to latest Early Carboniferous (Late Visean and Early Namurian). Montana, New Mexico, Algeria.

Etymology. The generic name is derived from *korys, korystos* (Greek), crested, and *schisma* (Greek), slit, referring to the strongly raised deltoid crests bearing hydrospire slits in this genus.

Discussion. Koryschisma is represented by an excellent collection of silicified material from the middle Lodgepole Limestone at Bandbox Mountain in west-central Montana, including about 145 complete or partial thecae, several hundred separate plates and ambulacral fragments, several hundred stem segments and individual columnals, and even a few brachiole fragments. Quality of the silicification is generally very good, making it easy to study the morphology, and the numerous separate plates have yielded additional information about internal features.

Koryschisma differs from other Devonian and Mississippian phaenoschismatids by having medium to high deltoid crests, two anal deltoids with the hypodeltoid occurring on the thecal surface, and medium-length ambulacra with the lancet partly exposed. It most closely resembles *Leptoschisma* and *Pleuroschisma* from the Devonian and *Phaenoschisma* and *Hadroblastus* from the Mississippian. It appears to be intermediate between these Devonian and Mississippian genera, as noted by Breimer and Macurda (1972, p. 219, textfig. 104).

Koryschisma differs from *Leptoschisma* by having only two anal deltoids, larger deltoid crests with more hydrospire slits exposed, somewhat wider ambulacra with the lancet partly exposed, and no BA axis in the basals. *Koryschisma* differs from *Pleuroschisma* by having only two anal deltoids, wider and less depressed ambulacra that conceal more hydrospire slits and have the lancet partly exposed, usually lower deltoid crests with fewer hydrospire slits, and other minor differences. *Koryschisma* differs from *Phaenoschisma* by having a prominent hypodeltoid on the thecal surface, usually narrower ambulacra having less of the lancet exposed and covering fewer of the hydrospire slits, and (in the type species) regular deltoids that barely appear on the thecal surface. *Koryschisma* differs from *Hadroblastus* by having a more elongate thecal shape, higher deltoid crests with depressed ambulacra, less exposure of the lancet, usually fewer hydrospire slits, some of which are concealed, and other differences.

Breimer and Macurda (1972, pp. 18–20, 217–221) and Macurda (1983, pp. 60–65) described some of the morphologic and growth features of *Koryschisma elegans* (then unnamed), and informally assigned two other phaenoschismatid species to this genus. We agree with their assignments, and have briefly diagnosed and compared these other two species (*Koryschisma saharae* and *K. parvum*) with the type species described here in detail.

KORYSCHISMA ELEGANS Sprinkle and Gutschick, new species

Plate 2, Figures 1–59;
Text-Figures 9 and 11–12

"New Lower Mississippian genus from Montana; Phaenoschismatid n. gen.; 'undescribed phaenoschismatid B' (UB); Phaenoschismatid, new genus, new species. Miss., Lodgepole Fm., Bandbox Mountain, Cascade Co., Montana, USA.; undescribed

phaenoschismatid genus; undescribed genus; 'X' . . . undescribed phaenoschismatid from Montana (UB); phaenoschismatid (UB) . . . from the Mississippian of Montana; phaenoschismatid UB," Breimer and Macurda, 1972, pp. 20, 219–221, 291–292, 312, 348, 362, and 366, textfigures 72, 100, and 104, table 2; Macurda, 1983, pp. 61–62 and 189, table 20.

Diagnosis. Theca large, obconical, L/W averages 1.39, pelvis somewhat longer than vault, V/P averages 0.67, pelvic angle averages 52°, crests moderately high with sharp raised edges, adoral edge of deltoids serrated, even with summit; ambulacra long, lanceolate, lancet about one-fourth of ambulacral width; 3–9 hydrospire slits per group, number slightly reduced on anal side; hypodeltoid prominent, hooded, other deltoids barely appearing on thecal surface, heavy secondary deposits at tip of basals; brachioles ridged; stem long with alternating flanged columnals, apparently attached distally using a recumbent rhizoid holdfast.

Description. About 145 partial and complete specimens plus about 500 separate plates, ambulacral pieces, stem segments and columnals, and brachiole segments available for study. Type specimens include holotype MCZ 915, 30 paratype thecae, including the 16-specimen growth series studied by Breimer and Macurda (1972), and 31 paratype fragments or plates.

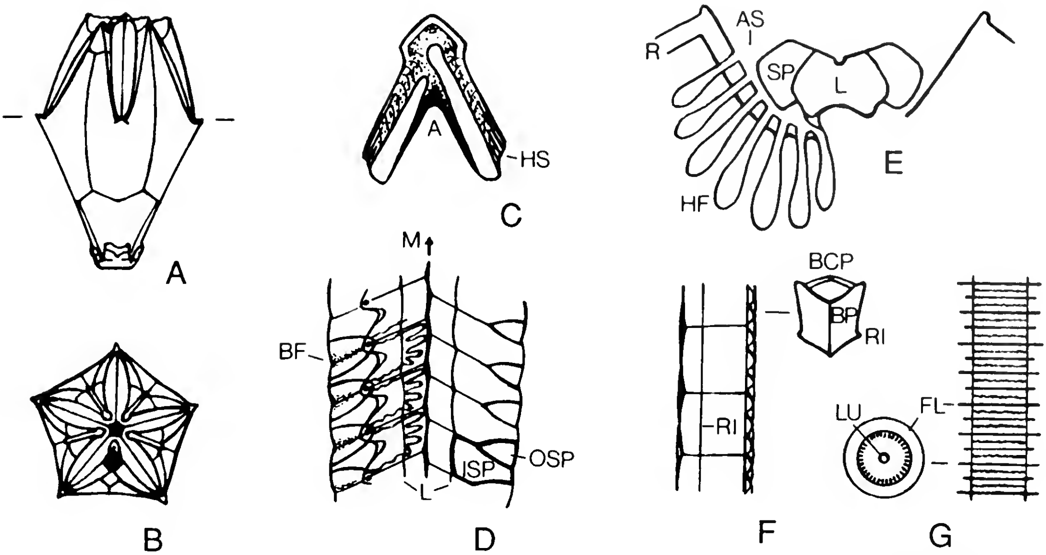
Theca obconical, pelvis longer than vault, maximum width at tips of ambulacra above midheight (Text-Fig. 11A), pelvis conical with nearly straight sides (basal profile very slightly convex, radial profile very slightly concave), stem facet relatively large with prominent secondary deposits, interambulacra nearly straight ignoring large radial lips, slightly concave with lips (Plate 2, Fig. 11). Holotype (largest theca in available collections; Plate 2, Figs. 1, 12–13) 19.0 mm long, 12.4 mm wide, with a vault 7.9 mm long and pelvis 11.2 mm long; smallest theca (Breimer and Macurda, 1972, textfig. 72.1) about 5.8 mm long and 4.8 mm wide. In eight complete MCZ thecae, L/W ratio ranges from 1.27 to 1.53 and averages 1.39, V/P ratio ranges from 0.48 to 0.80, averaging 0.67, and pelvic angle ranges from 42° to 58° and averages 52°. Summit nearly flat with sharp and fluted adoral deltoid edges.

Basals three, medium-sized forming about 40% of pelvis, normally arranged, two larger and one smaller (azygous), azygous basal elongate pentagonal, larger basals hexagonal; in large basal set (Plate 2, Figs. 46–48), azygous basal 5.7 mm long, 4.7 mm wide, larger basal about same length and 5.7 mm wide; stem facet formed by prominent secondary deposits bridging over triangular tip of basals to form large, nearly circular platform bearing stem facet with small central lumen. Oblique deep depression about 0.8–1.0 mm long near middle (C ray) of BD basal about 1.0 mm from stem lumen (Plate 2, Fig. 42), apparent site of internal organ near thecal base.

Radials five, large, forming most of thecal surface and 60% of pelvis, RD axis greater than RB axis at all sizes; each radial roughly rectangular with deep ambulacral sinus in adoral end, sides convex, profile convex with large radial lip at origin continuing pelvis profile; each ambulacrum strongly depressed below edge of radial sinus, which has sharp raised ridge about 1 mm higher than plate surface (Plate 2, Figs. 14–15).

Regular deltoids four, small, crested, barely reaching thecal surface (tiny V-shaped external DR growth sector just aboral to end of crest), crests horizontal on summit with wavy, serrated, or "cockscomb" edge, forming incipient paired spiracles adorally behind small deltoid lip (Plate 2, Fig. 11), small spine often on lip between spiracles, mouth rounded pentagonal, about 1.2 mm in diameter in large specimen, radials strongly overlap deltoids at top of sinus but overlap slightly reversed at and below edges of ambulacra (Plate 2, Fig. 32).

Anal deltoids two, medium-sized epideltoid with long depressed limbs and small diamond-shaped hypodeltoid on thecal surface. Epideltoid inverted V-shaped, lip



Text-Figure 11. Morphology of *Koryschisma elegans,* n. gen., n. sp. A–B, side and summit views of a large theca based on holotype MCZ 915 and paratype MCZ 916 showing greatest width (short lines) above midheight, enlarged hypodeltoid appearing on thecal surface, and heavy secondary deposits forming stem facet. C, much-enlarged epideltoid based mostly on paratype MCZ 949; note location of anus (A), adoral ends of hydrospire slits (HS) on limbs, and ridge on right limb extending further adoral than left limb. D, enlarged view of ambulacrum in paratype MCZ 942 showing central lancet (L) and inner and outer side plates (ISP and OSP) bearing brachiole facets (BF) at the edge; small arrow points toward mouth (M). E, enlarged cross section of ambulacrum and adjacent radial (R) drawn mostly from paratypes MCZ 956, MCZ 942 (inside of ambulacrum), and MCZ 924 (hydrospires); note side plates (SP) wrapping around edge of central ridged lancet (L) with slits in the ambulacral sinus (AS) leading to internal hydrospire folds (HF). F, much-enlarged side view and cross section of isolated brachiole fragment MCZ 959 showing ridge (RI) on biserial brachiolar plates (BP) and tiny brachiolar cover plates (BCP). G, much-enlarged side view and columnal face of proximal stem segment MCZ 931; note equatorial flange (FL) on alternating columnals and smaller central lumen (LU).

slightly wider than other deltoid lips, limbs infolded into hydrospires with folds extending from limbs into space for hindgut, adorally ridge from "C" limb slightly higher than that for "D" limb (Text-Fig. 11C; Plate 2, Figs. 17, 30). Hypodeltoid greatly enlarged over other deltoid bodies with large external HDR sector, slightly to moderately hooded, adoral edge projecting slightly above other deltoid crests and summit (Plate 2, Figs. 14, 21), forms aboral side of elliptical anus slightly larger than mouth (1.8 mm long in 18 mm long theca), forms strongly convex sutures with radials, grows aborally from near tip of hood.

Ambulacra five, relatively long, moderately wide, lanceolate, moderately convex in cross section, slightly curved in profile, lancet slightly exposed in center, one-third to one-half of its width and one-fourth of ambulacral width, side plates curve around lateral edges of lancet (Text-Fig. 11E; Plate 2, Figs. 18, 34, 37), lancet grooved at bottom with adoral keel, inner side plates large, constricted abmedially, outer side plates small, rounded triangular, notch abmedial aboral edge of inner side plate, inner and outer side plates form brachiole facet at abmedial edge of ambulacrum, brachiolar pit small, at end of side food groove on side plate suture (Text-Fig. 11D), brachiolar facets together hemielliptical, about 0.25 mm long, canted toward each other so that deepest part between them on side plate suture. Side food grooves enter main food groove at 45–70° angle, four lobes per side plate along main food groove, 3–5 adorally and two small lobes aborally along side food grove.

Oral cover plates present on summit of one paratype (UMMP 60694; Plate 2, Fig. 38), form five domed covers about 0.4 mm

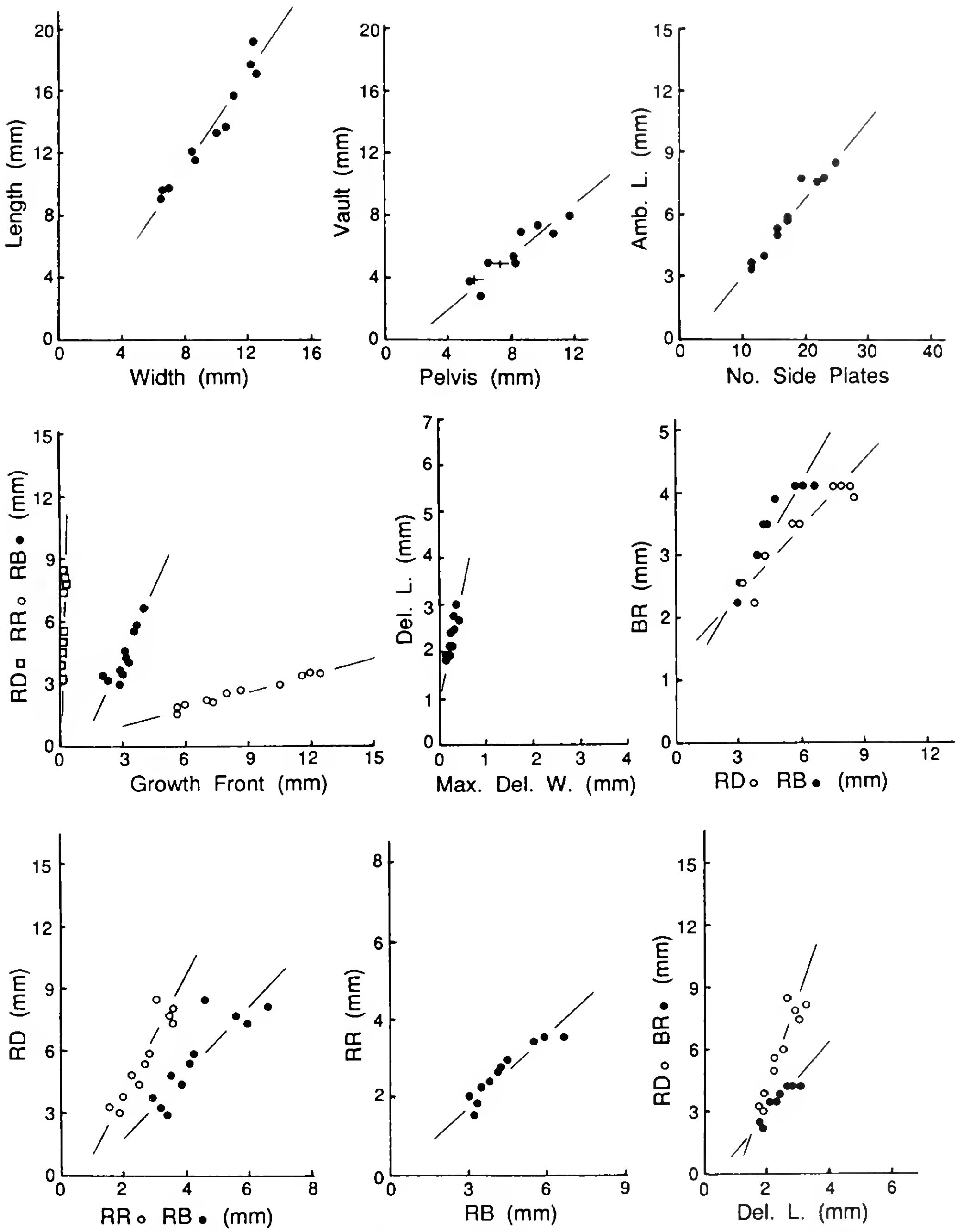
high and 0.6 mm wide made up of tiny plates about 0.15 mm in size over adoral ambulacra converging at mouth. Symmetry appears pentagonal over mouth with no apparent "2-1-2" arrangement in covers. Several paratypes (especially UMMP 65893) show remnants of small spines about 0.6 mm long and 0.15 mm in diameter near mouth and anus (Plate 2, Fig. 38), apparently to protect these summit structures.

Hydrospires in 10 groups, slits partly exposed in sinus and crest walls, mostly hidden beneath ambulacra, 3–9 folds per normal group, number slightly reduced on anal side to 2–7 folds; lower folds hang down into thecal cavity, deepest at radiodeltoid suture (Plate 2, Figs. 16, 33), upper folds extend laterally in from sinus edges, short slit and fold at top of sinus (Plate 2, Fig. 15) probably added late in growth; in internal view folds bend abmedially at radiodeltoid suture, folds pinched together at aboral end near radial origin (Plate 2, Fig. 16); adoral edges of ambulacra form incipient spiracles at adoral edge of deltoid crests.

Ornament consists of fine to medium-strength growth lines parallel to margins on basals and radials, stronger growth lines on RHD front (Plate 2, Figs. 15, 17), very fine growth lines on hypodeltoid and sides of deltoids. Several heavy layers of secondary deposits over origins of basals to produce large circular platform for stem attachment from smaller triangular tip of basal cone (Plate 2, Figs. 40–42, 46–47, and 49); secondary deposits also forming large, pointed, radial lip up to 1.5 mm long that continues pelvic profile, lip covers few growth lines at origin of each radial, and bears median raised ridge adorally to separate brachiole groups (Plate 2, Figs. 12, 17). Thin 1 mm high ridge of secondary calcite along edge of each ambulacral sinus above plate surface (Plate 2, Figs. 15, 27); several lateral-pointing spines of apparent secondary calcite on adoral-most side plates (Plate 2, Fig. 34); and small spine of secondary calcite on some deltoid and epideltoid lips.

Disarticulated stem material abundant (Text-Fig. 9); distinctively flanged and somewhat heteromorphic proximally, developing cirri and rootlets distally. Longest stem segment 22 mm long with 33 columnals (Plate 2, Fig. 56); one short stem segment attached to small basal set (Plate 2, Fig. 59); one theca had single columnal attached but lost it during etching. Proximal columnals thin, wide, with a large flange (Plate 2, Figs. 52, 54, and 56); typical proximal columnal 0.4 mm long, 1.6 mm wide, having a circular equatorial flange 2.5–3.0 mm in diameter; columnal faces round with 49–50 small crenulae around margin and small, nearly circular lumen 0.1 mm in size in center (Text-Fig. 11G). Two or three sizes of flanged columnals alternating in proximal stem, either in sequence "lg.-sm.-med.-sm., lg.-sm.-med.-sm., . . ." or as "lg.-sm., lg.-sm., . . ." (Plate 2, Figs. 54, 56). Distal columnals longer (0.5–0.7 mm long), narrower (1.2–1.3 mm wide), with smaller flanges (1.3–1.5 mm in diameter) that alternate somewhat in size and appear partly covered by subsequent lateral growth of columnals (Plate 2, Fig. 55). Cirri (rootlets?) attached to distal columnals on flanges or sutures (Plate 2, Fig. 58), most cirrals about 0.25 mm long, 0.5–0.8 mm in diameter, with faces bearing 11–14 small crenulae. Cirri apparently concentrated on one side of best distal stem segment (Plate 2, Fig. 58), implying a recumbent rhizoid holdfast (Brett, 1981, pp. 348, 351). Total length of stem unknown, but hardly any gradation in size or morphology noted in longest preserved segments.

Brachiole segments up to 6 mm long also preserved in acid residues (Plate 2, Figs. 23–24); brachioles ridged, roughly pentagonal in cross section, biserially plated (Text-Fig. 11F); brachiolar plates about 0.3 mm long, 0.33 mm wide, and 0.15 mm deep (across food groove), possibly one biserial set of slightly domed, triangular, brachiolar cover plates over shallow, V-shaped food groove (Text-Fig. 11F), about three brachiolar cover plates per brachiolar plate on each side.



Text-Figure 12. Growth plots for 11 measured specimens (MCZ 915–923 plus two extras) of *Koryschisma elegans*, n. gen., n. sp., set up in a similar format to that used by Breimer and Macurda (1972, textfig. 72) for this same (then unnamed) species. Differences include the addition of a graph for vault vs. pelvis (top center), lower values for the RD growth front and maximum deltoid width (because we measured only the small external part on the thecal surface), and a different order to the plots. Best-fit lines in all plots were hand fit, and short lines with a central tick mark (top center) indicate estimated values in broken specimens.

Growth features described by Breimer and Macurda (1972, p. 219, textfig. 72) and in Text-Figure 12; their growth series specimens ranging from 5.8 to 12.5 mm in length, ours from 9.0 to 19.0 mm. One abnormal individual (UMMP 60688) found in 145 studied specimens (0.7%); D ambulacrum absent from its ambulacral sinus and E ambulacrum triserial, wider than normal, with two main food grooves (D? and E) running most of length (Plate 2, Fig. 39).

Studied Specimens. Holotype MCZ 915, paratypes MCZ 916–961 (15 complete or partial thecae, 9 stem segments or columnals, 20 separate plates and ambulacral fragments, 3 brachiole segments) and UMMP 60679-60694 and 65893 (16 complete specimens measured by Breimer and Macurda [1972] plus one other theca). Additional material in collections MCZ 962 and 1062 and UMMP 1970/M-171.

Etymology. Elegans (Latin), choice, fine, refers to the excellent preservation shown by the silicified specimens of this species.

Occurrence. All material (except for one possible basal plate) from the middle Lodgepole Limestone about 170–175 ft (52–53 m) above the base of the Paine Member, on the west face of Bandbox Mountain, Little Belt Mountains, west-central Montana (see Text-Fig. 5). MCZ 1062, a basal plate with distinctive secondary deposits that may belong to this species, is from the upper Lodgepole Limestone (Woodhurst Member) about 655 ft (200 m) above the base at Sacagawea Peak, Bridger Range, southwestern Montana.

Discussion. Koryschisma elegans is most closely related to the forms described as *Phaenoschisma? saharae* Breimer and Macurda (1972, pp. 18–20), Macurda (1983, pp. 61–65) and *Phaenoschisma? parvum* Macurda (1983, pp. 60–61), which are here reassigned to *Koryschisma* as separate species. *Koryschisma elegans* differs from *K. parvum* by having a larger and more elongate theca (higher L/W ratio), wider crests, more hydrospire slits, and is slightly older (Kinderhookian vs. Osagean).

→

PLATE 3

Figures 1–16. *Orophocrinus macurdai* Sprinkle and Gutschick, n. sp., lower Paine Member, lower Lodgepole Limestone, 1, 3, 5, 9, 11, and 13–16 from Milligan Canyon East, 2, 4, 6–8, 10, and 12 from Dry Hollow, southwestern Montana. 1, B-side view of smallest paratype MCZ 812, ×2.3; 2, 8, B-side and top views of small conical paratype MCZ 813 showing large stem facet, ×2.3; 3, 9, E-side and top views of small wide paratype MCZ 815; note convex ambulacra and spiracular slits, ×2.3; 4, 10, B-side and top views of medium paratype MCZ 817 showing missing hypodeltoid, ×2.3; 5, 11, C-side and top views of medium paratype MCZ 818; note conical shape and relatively short ambulacra, ×2.3; 6, E-side view of medium wide paratype MCZ 821, ×2.3; 7, C-side view of large, slightly-crushed paratype MCZ 822 showing convex ambulacra and coarse HD ornament on C radial, ×2.3; 12, top view of medium paratype MCZ 819 with hypodeltoid still in place, ×2.3; 13–16, E-side, BC-side, top, and oblique top, respectively, of very large crushed holotype MCZ 811 in slab; note missing basals, growth lines on radials, long lanceolate ambulacra, and hypodeltoid in place over anus, ×2.3 and ×3.

Figures 17–24. *Orophocrinus* cf. *O. gracilis* (Meek and Worthen), lower Paine Member, lower Lodgepole Limestone, 17–18, and 22–24 from Standard Creek, 19–20 from Dry Hollow, and 21 from Little Antelope Creek, southwestern Montana. 17–18, AB-side and top views of smallest apparent specimen MCZ 840 showing weathered pelvis and longer ambulacra than 1–6 above, ×2.3; 19–20, front and back of medium, vertically-crushed specimen MCZ 838 in slab; note long ambulacra and trace of internal hydrospires, ×2.3; 21, side view of large, badly-crushed specimen MCZ 839 showing long ambulacra and growth lines on radials, ×2.3; 22–24, front, separate ambulacrum and deltoid from front, and back of large crushed and eroded specimen MCZ 836 in slab; note thecal shape, long ambulacra, vault longer than pelvis, and deltoid shape, ×3.

Figures 25–27. *Orophocrinus* sp., Woodhurst Member, upper Lodgepole Limestone, Baldy Mountain, Bridger Range, southwestern Montana; top, E-side, and basal views of medium-sized specimen MCZ 884 showing badly-etched surface, thecal shape, concave ambulacra, and small hole in basal (27), ×2.5.

Figure 28. *Phaenoschisma*? sp., float from Woodhurst Member, upper Lodgepole Limestone, Saddle Peak, Bridger Range, southwestern Montana; side view of small specimen MCZ 885 before excavation from slab; note elongate shape and short ambulacra, ×6.

Figure 29. *Hadroblastus* sp., float from middle Lodgepole Limestone, Standard Creek, southwestern Montana; side view of partly-excavated specimen MCZ 748 showing crushed theca, fully-exposed hydrospires, attached proximal stem, and few brachioles from left ambulacrum, ×2.

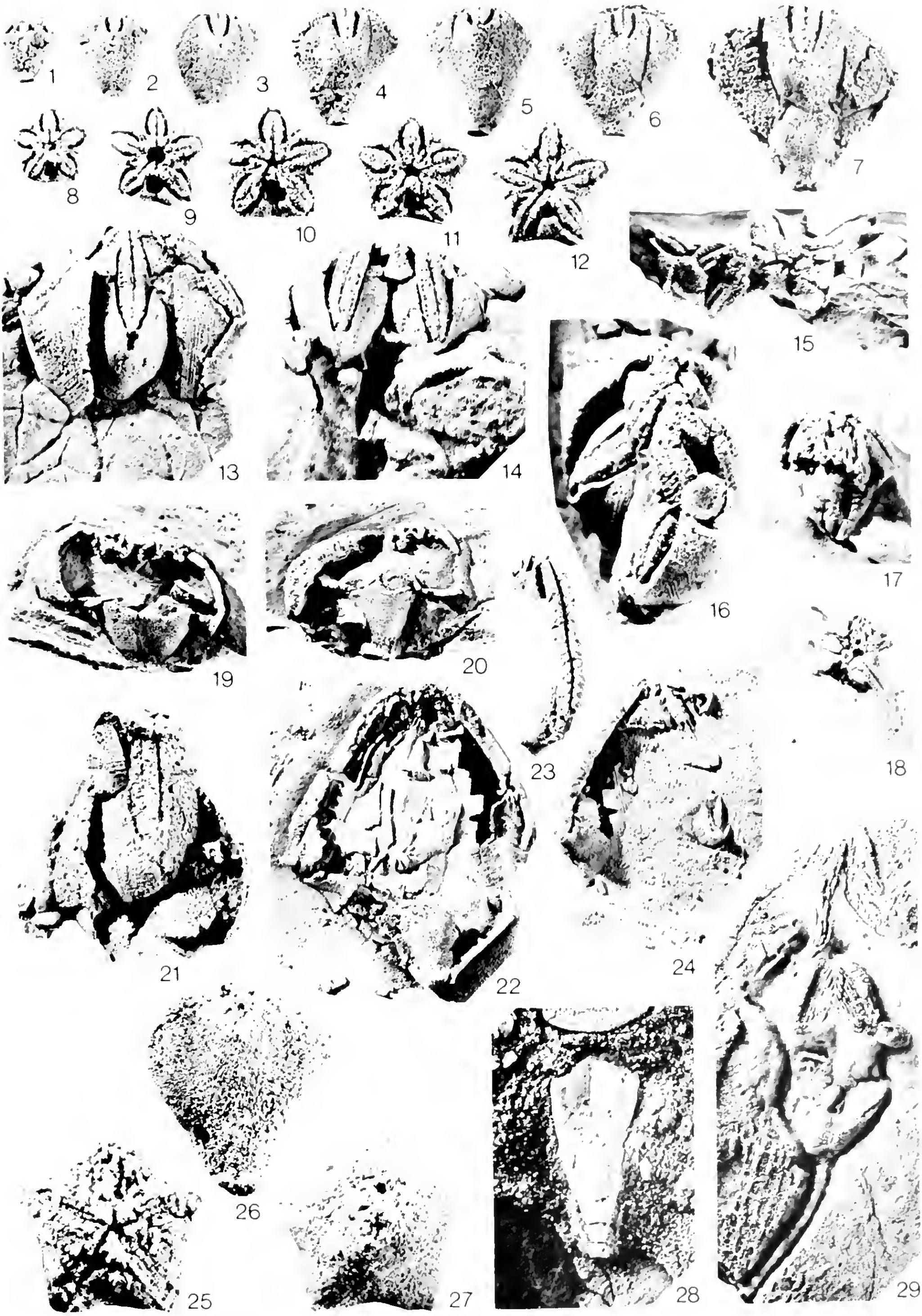

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TABLE 4. MEASUREMENTS FOR LODGEPOLE BLASTOID SPECIES THAT HAD FOUR OR FEWER MEASURABLE SPECIMENS. MEASUREMENTS ARE THE SAME AS THOSE USED FOR THE GROWTH PLOTS (FOR EXAMPLE, SEE →

Species and specimen number	Length (mm)	Width (mm)	Vault (mm)	Pelvis (mm)	Pelvic angle	St fac. (mm)	BR axis (mm)	RB axis (mm)
Phaenoschisma? sp.								
MCZ 885	5.2	~3.2	~0.6	~4.6	45°	~0.8	>2.9	~2.0
Hadroblastus sp.								
MCZ 748	16.2	~12.0	6.0	10.1	—	1.1	~6.1	~4.4
Orophocrinus cf. *O. gracilis*								
MCZ 840	6.8	6.5	2.6	4.2	~65°	~1.2	~2.4	~2.0
MCZ 836	16.1	~15.1	8.7	7.5	~95°	1.6	4.6	>4.3
MCZ 838	—	—	—	—	~70°	2.3	4.6	~6.5
MCZ 839	—	—	~10.0	—	—	—	—	>6.0
Orophocrinus sp.								
MCZ 884	14.0	13.1	4.8	9.2	75°	2.8	4.0	5.5
Metablastus milliganensis								
MCZ 804	~11.0	6.4	5.7	5.2	~60°	—	~3.5	2.9
MCZ 803 (Holotype)	11.0	6.6	4.6	6.4	~55°	0.8	3.7	3.2
MCZ 805	~13.7	8.2	6.0	~7.7	~50°	—	—	—
Montanablastus baldyensis								
MCZ 889	6.4	5.0	3.0	3.3	~75°	~0.6	1.8	1.6
MCZ 893	7.7	~5.6	3.8	3.9	~65°	0.7	1.9	2.0
MCZ 886 (Holotype)	8.6	6.5	5.1	~3.6	80°	~0.9	1.9	2.3
MCZ 892	10.2	7.3	5.7	5.1	75°	0.7	2.5	2.8

Koryschisma elegans differs from *K. saharae* by being less elongate (lower L/W ratio), having a higher V/P ratio, higher crests with wider ambulacra, a longer, more pointed hypodeltoid, and by being considerably older (Late Tournaisian equivalent vs. Late Visean to Early Namurian).

KORYSCHISMA SAHARAE (Breimer and Macurda), 1972

Pentremites sp., Pareyn, 1961, pp. 223–224.
Phaenoschisma? saharae, "*Phaenoschisma*" *saharae*, Breimer and Macurda, 1972, pp. 18–20, 387, plate II, figures 4–5 and 10; Macurda, 1983, pp. 61–65, plate 14, figures 1–13, table 21.

Diagnosis. Theca large, elongate conical, L/W averages 1.71, pelvis much longer than vault, V/P averages 0.23, pelvic angle averages 38°; deltoid crests low to medium, hypodeltoid large, other deltoids appear confined to ambulacral sinuses; ambulacra nearly linear, lancet making up about one-fourth of width; 5–9 hydrospire slits per group, number reduced by about one-third on anal side; subdued secondary deposits at tip of basals.

Discussion. This species, from the Late Visean and Early Namurian of Algeria, is larger and more elongate than *K. elegans* and *K. parvum*, with a shorter vault, narrower ambulacra, lower crests, and more subdued secondary deposits around the large stem facet.

KORYSCHISMA PARVUM (Macurda), 1983

"UA (undescribed phaenoschismatid A . . .); phaenoschismatid (UA)," Breimer and Macurda, 1972, pp. 217–219, plate IV, figures 17, 20, plate V, figures 1–2, textfigure 71.
Phaenoschisma? parvum, Macurda, 1983, pp. 60–61, plate 13, figures 9–10, 14–17, 19–20, 23–24, table 19.

Diagnosis. Theca small, widely biconical, L/W averages about 1.1, pelvis longer than vault, V/P averages about 0.57, pel-

(*continued*) TEXT-FIGURE 12). A ~ PRECEDING A NUMBER INDICATES THAT THIS MEASUREMENT WAS ESTIMATED IN A DAMAGED, INCOMPLETE, OR CRUSHED SPECIMEN; SPECIMENS WITH A — WERE TOO INCOMPLETE OR DAMAGED TO MEASURE.

RR front (mm)	RR axis (mm)	RR front (mm)	RD axis (mm)	RD front (mm)	Del. len. (mm)	Del. wid. (mm)	Amb. len. (mm)	Amb. wid (mm)	No. of side pls.
~1.1	0.9	2.0	~1.0	—	—	—	~1.5	~1.0	—
~4.6	3.3	5.6	4.7	2.3	~4.5	~4.3	~6.5	~1.2	>18
—	2.0	—	3.0	0.4	1.4	0.9	4.2	1.0	15
—	~4.3	—	7.2	1.2	3.0	2.1	>9.2	>1.3	~19
~4.5	5.0	~7.0	7.1	1.3	—	~2.2	>9.0	~2.0	>20
—	5.5	>9.2	9.2	1.2	4.9	2.4	11.2	1.7	28
~4.5	4.1	~8.0	~5.0	1.6	3.5	2.0	7.1	1.7	~29
2.5	1.8	7.3	5.5	<0.1	<0.1	<0.2	5.4	0.8	~19
2.5	1.9	6.9	5.7	<0.1	<0.1	<0.2	5.1	0.7	20
2.5	—	—	~6.9	<0.1	<0.1	<0.2	6.5	0.7	~23
1.5	1.1	3.7	3.0	~0.2	0.7	~0.4	2.9	0.8	13
1.8	1.6	~5.0	3.9	—	~0.7	—	4.3	1.0	15
2.2	1.7	5.7	4.7	~0.3	0.9	0.6	4.6	1.0	16
~2.8	2.2	~7.0	5.6	0.8	~1.9	~0.9	6.2	>0.7	~15

vic angle averages 67°; deltoid crests high, slope down to mouth, hypodeltoid relatively large, on thecal surface, other deltoids confined to ambulacral sinuses; ambulacra lanceolate, lancet only slightly exposed in center; 4–6 hydrospire slits per group, number slightly reduced on anal side.

Discussion. This species, from the Osagean of New Mexico, is smaller and much wider than *K. elegans* and *K. saharae*, with a shorter vault, higher deltoid crests, and fewer hydrospire slits. Because of its small size, it may be a paedomorphic derivation of the slightly older *K. elegans*.

Genus PHAENOSCHISMA Etheridge and Carpenter, 1886

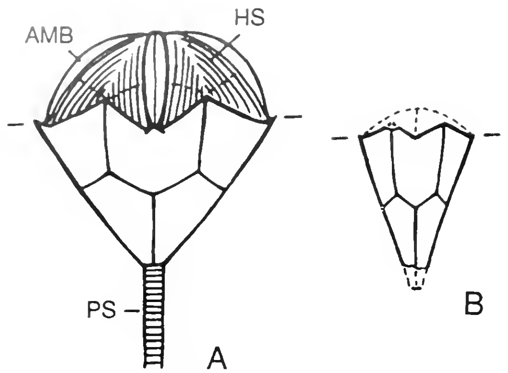
Type Species. *Pentatrematites acutum* Sowerby, 1834.

Diagnosis. Fissiculate blastoids with a conical to obconical theca; 10 hydrospire groups having slits partly exposed, number of slits slightly reduced on anal side; two anal deltoids, hypodeltoid small, not on thecal surface; ambulacra lanceolate, lancet widely exposed.

Occurrence. Early to Middle Mississippian, central and western U.S.A., Early Carboniferous, England and Ireland.

PHAENOSCHISMA? SP.
Plate 3, Figure 28;
Text-Figure 13B; Table 4

A single small specimen of an apparent phaenoschismatid was found in the float near the top of the Lodgepole Limestone at Saddle Peak in the Bridger Range. It was preserved as a crushed but nearly complete calcitic theca on a slab (Plate 3, Fig. 28); the theca was extracted using an air abrasive unit, but unfortunately it proved to be incomplete with only the basals and radials still preserved. Theca about



Text-Figure 13. A, reconstructed side view of *Hadroblastus* sp. based on MCZ 748; note thecal shape (greatest width at short lines), wide ambulacral sinuses with hydrospire slits (HS) exposed, curved raised ambulacra (AMB), and size of proximal stem (PS), ×1.8. B, slightly reconstructed side view of *Phaenoschisma*? sp. (MCZ 885) showing shape (greatest width at short lines), long basals and radials, and inferred shape of missing vault with short ambulacra, ×3.8.

5.0 mm long with incomplete base and missing deltoids and ambulacra, original length at least 5.2 mm, maximum width (crushed) 3.9 mm, original width estimated at 3.2 mm; pelvis about 4.6 mm long and incomplete vault at least 0.6 mm long. L/W ratio probably near 1.5–1.6 originally, V/P ratio about 0.13 originally, and pelvic angle now 40° on crushed side.

Pelvis conical, straight to slightly concave in profile; basals three, appear normally arranged with two larger, one smaller, pointed at top, occupy 50–60% of preserved pelvis, about 2.9 mm long with small amount added for missing stem facet; stem facet slightly triangular, secondary deposits not observed. Radials five, pentagonal, occupy slightly less of pelvis than basals, notched at top for ambulacra and deltoids, notch on apparent posterior side larger than others implying external hypodeltoid possibly present (Text-Fig. 13B), regular deltoids small.

No deltoids or ambulacra preserved, only ends of hydrospire slits on adoral edges of radials, apparently at least four hydrospire slits per ambulacral side. Other summit structures unknown.

The only theca is MCZ 885 which was found in the float about 100–200 ft (30–61 m) below the top of the Lodgepole Limestone at Saddle Peak, southern Bridger Range, southwestern Montana.

Discussion. This single specimen is too incomplete to tell whether it belongs to the genus *Phaenoschisma*, but this is considered the most likely possibility based on its preserved morphology and Early Mississippian age. It is rather similar in side view to *P. laevisculum* and to *P. gracillimum* (see Breimer and Macurda, 1972, plate 3, figures 14, 19, and 26–27), both from the similar-aged Burlington Limestone. These species are somewhat larger, differ slightly in their thecal proportions, and do not have an enlarged hypodeltoid contributing to the posterior thecal surface. This is the only relatively complete theca of a possible *Phaenoschisma* known from the Lodgepole Limestone, but a few elongate basals perhaps belonging to a similar blastoid are also known from the lower fauna in the Allan Mountain Limestone at the North Sawtooth Mountain Section in northwestern Montana.

Family NEOSCHISMATIDAE Wanner, 1940
Genus HADROBLASTUS Fay, 1962c

Type Species. Hadroblastus convexus Fay, 1962c.

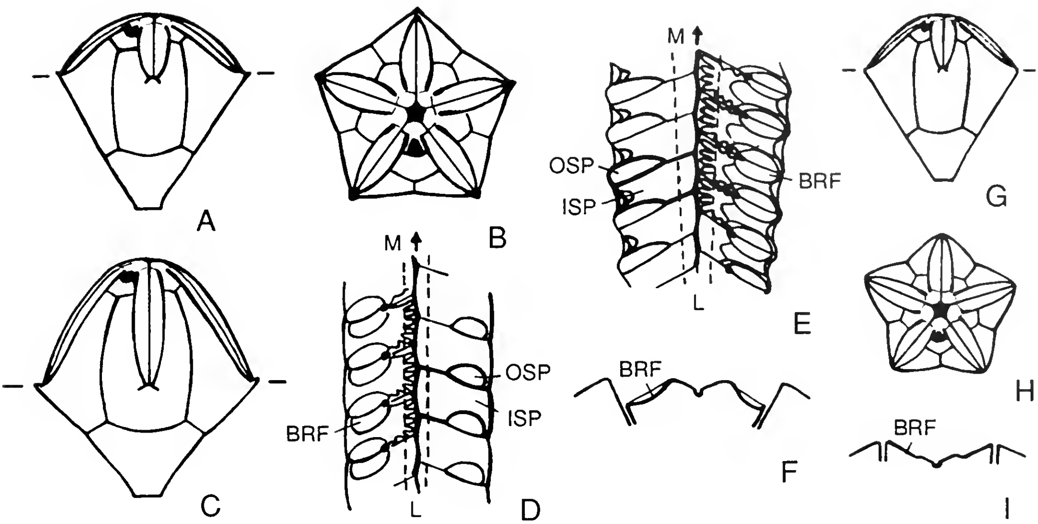
Diagnosis. Fissiculate blastoids with biconvex theca, vault usually shorter than pelvis, deltoid crests low to medium; 10 hydrospire groups, slits almost completely exposed in wide shallow sinuses alongside ambulacra, slits usually reduced on anal side; two anal deltoids, epideltoid forms anal hydrospires, hypodeltoid forms part of theca wall; ambulacra lanceolate, often raised, lancet exposed throughout length.

Occurrence. Early to Middle Mississippian, central and western U.S.A.; Early Carboniferous, Ireland? and Scotland?

HADROBLASTUS SP.
Plate 3, Figure 29;
Text-Figure 13A; Table 4

Hadroblastus sp., Breimer and Macurda, 1972, pp. 30, 382, plate 18, figure 1.

A single specimen from an unknown position in the middle Lodgepole Limestone was found at Standard Creek, southwest-



Text-Figure 14. Morphology of *Orophocrinus macurdai*, n. gen., n. sp., (A–B, E–F), *Orophocrinus* cf. *O. gracilis* (Meek and Worthen) (C–D), and *O.* sp. (G–I). A–B, side and summit views of a large theca (based on MCZ 821 and holotype MCZ 811) showing shape, maximum width (short lines), fairly wide ambulacra with spiracular slits alongside, slightly concave interambulacra, and size and shape of hypodeltoid. C, reconstructed side view based on MCZ 836 showing shape, longer ambulacra, and location of greatest width (short lines) near midheight. D, enlarged plan view of ambulacrum in MCZ 836 showing lancet (L) slightly exposed in center (small arrow points toward mouth [M]), large inner and small outer side plates (ISP and OSP) occupying most of width and supporting a brachiole facet (BRF) near edge, ×9.5. E–F, enlarged plan view and cross section of ambulacrum in paratype MCZ 823; note lancet (L) exposed in center, large inner and small elongate outer side plates (ISP and OSP) together supporting an elliptical brachiole facet (BRF), well-developed cover plate lobes and sockets, and convex cross-sectional shape with depressed, outward-slanting facets, ×11.8. G–H, side and summit views of MCZ 884 showing similarity in thecal shape to A and B except for more concave interambulacra. I, cross section of E ambulacrum in MCZ 884 showing concave surface with inward-slanted brachiole facets (BRF) quite different from F, ×7.1.

ern Montana. This specimen was figured by Breimer and Macurda (1972) using a pre-preparation photograph supplied by Sprinkle in 1966. Subsequently, the specimen was partly uncovered using an air abrasive unit although the matrix proved too hard and deep to uncover an entire side (Plate 3, Fig. 29). Part of the proximal stem was also found still attached to the theca.

Description. Only known specimen partly buried and crushed on slab with exposed plates silicified. Theca fairly large, apparently biconvex, 16.2 mm long, at least 12 mm wide (incomplete but crushed), vault 6.0 mm long, pelvis 10.1 mm long, L/W ratio approximately 1.35 based on exposed width, V/P ratio 0.59. Pelvic angle difficult to measure, perhaps 70–80° originally (Text-Fig. 13A).

Basals fairly long, occupying 50–60% of pelvis, at least 7 mm long, azygous basal quadrate in shape, about 3.5 mm wide. Radials fairly large, about 6.5 mm long, perhaps as much as 6.5 mm wide, radial body about 4.5 mm long, shallow ambulacral sinuses about 2 mm long. Deltoids difficult to see, occupying broad ambulacral sinuses, approximately 3.5 mm long and about 3.5 mm wide, little or no deltoid crest present. Ambulacra occupying centers of broad ambulacral sinuses, at least 6.5 mm long and about 1.2 mm wide, appear to be flat to slightly convex in cross section, strongly convex in lateral view and considerably raised above surrounding sinuses (Text-Fig. 13A), too highly silicified to distinguish lancet or side plates. Hydrospires fully exposed, apparently 7–8 per ambulacral side, longest slits extending nearly full length of adjacent ambulacra, slits converge at center-line of deltoid which is not raised into crest above sinuses.

Few brachioles attached to left ambu-

lacrum in this specimen, brachioles incomplete, about 10–11 mm long, approximately 0.3 mm wide and deep, poorly preserved because of partial silicification (Plate 3, Fig. 29).

Proximal stem attached to facet on basals, preserved stem about 12.5 mm long extending off edge of slab (Plate 3, Fig. 29), about 1 mm in diameter both proximally and distally, made up of at least 47 columnals varying from about 0.17 mm long proximally to about 0.33 mm long distally.

Ornament on thecal plates difficult to see because of silicification and abrasion of plates during preparation, no trace of coarse ornament or growth lines.

Material and Occurrence. Only known specimen is MCZ 748 from an unknown height in the middle Lodgepole Limestone, slab found in the float above the lower cliffs containing *Tanaoblastus* at Standard Creek, Gravelly Range, southwestern Montana.

Discussion. This blastoid from the middle Lodgepole Limestone may represent a new species of *Hadroblastus*, but is not named here because the only known specimen is not well preserved or exposed. This form is larger and more elongate than the type species *H. convexus* Fay (1962c), which has a small squat theca with a low vault and moderate deltoid crests. It has a higher vault with lower deltoid crests than *H. breimeri* Ausich and Meyer (1988). It differs from *H. whitei* by having longer hydrospire fields without deltoid crests and perhaps fewer slits (7–8 vs. 9–10). It may have been similar to *H. blairi*, especially in ambulacral height and curvature, but was less squat and had almost no deltoid crests.

Family OROPHOCRINIDAE Jaekel, 1918
Genus OROPHOCRINUS von Seebach, 1864

Type Species. Pentremites stelliformis Owen and Shumard, 1850.

Diagnosis. Fissiculate blastoids having a conical, conoidal, or parachute-shaped theca, ten long spiracular slits and hydrospire groups alongside ambulacra; 4–11 hydrospire folds per group; two anal deltoids present, relatively small epideltoid with long aboral limbs and relatively small hypodeltoid visible on thecal surface; ambulacra relatively wide, usually raised, lancet narrowly exposed along much of length.

Occurrence. Early to Middle Mississippian, central, southwestern, and northwestern United States; Early Carboniferous (Tournaisian and Visean), Belgium, Great Britain, and Ireland.

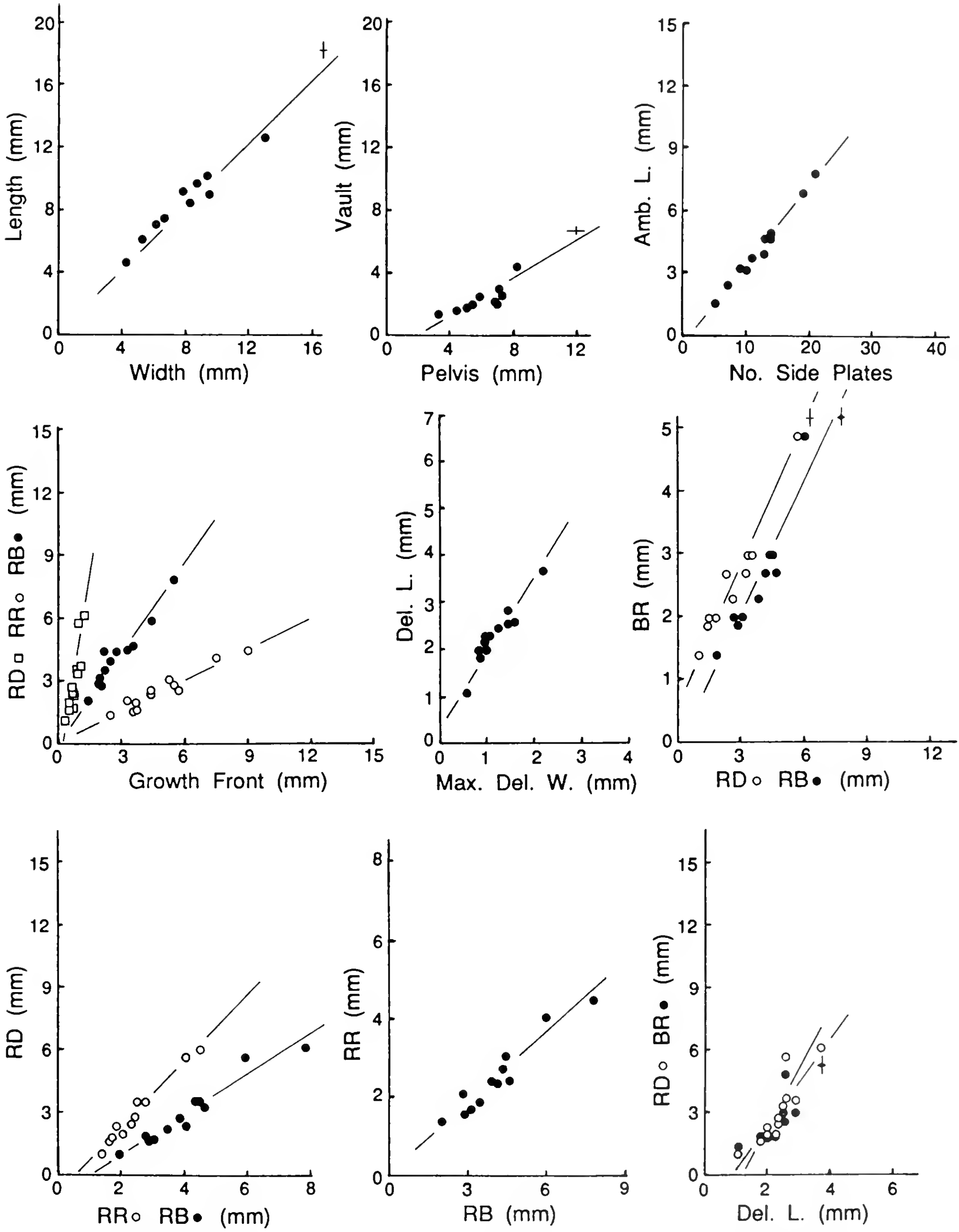
Discussion. Two species of *Orophocrinus* occur in the lower Lodgepole Limestone, and an additional specimen of a third species occurs in the upper Lodgepole Limestone of southwestern Montana. These occurrences extend the geographic range of this genus into the northwestern United States. *Orophocrinus* is a very wide-ranging genus in the Mississippian (Early Carboniferous) known from both North America and Europe. It differs from similar genera in the Orophocrinidae such as *Brachyschisma* by having a full set of anal hydrospires and only two anal deltoids, from *Katoblastus* by having the hydrospire slits completely hidden and only two anal deltoids, and from *Pentablastus* and *Acentrotremites* by having a different thecal shape with ambulacra that do not usually extend down the theca.

OROPHOCRINUS MACURDAI Sprinkle and Gutschick, new species

Plate 1, Figure 2; Plate 3, Figures 1–16; Text-Figures 14A–B, E–F, and 15

Diagnosis. Theca conical, L/W ratio averaging 1.07, V/P ratio averaging 0.29, pelvic angle averaging 64°, interambulacra flat to slightly concave, RD axis less than RB axis at all sizes, hypodeltoid widely borders spiracular slits, ambulacra strongly convex, brachiolar facets abmedial, usually five hydrospire folds per ambulacral side.

Description. Forty-one specimens and fragments available for study; description based on holotype MCZ 811, 11 additional



Text-Figure 15. Growth plots for the 12 measured specimens (MCZ 811–822) of *Orophocrinus macurdai*, n. sp. Best-fit lines in all plots were hand fit, and short lines with central tick mark represent estimates for large incomplete holotype MCZ 811 that lacks basals.

complete paratypes in growth series, and 12 other paratype specimens and fragments. Theca conical, made up mostly of conical pelvis with straight to slightly convex sides, capped by convex vault (Text-Fig. 14A); growth series specimens ranging from 4.5 mm long to incomplete holotype 13.2 mm long (no basals; original complete length estimated at 18.2 mm). In 12-specimen growth series, L/W ratio ranging from 0.88 to 1.18 and averaging 1.07, decreasing slightly during growth; V/P ratio ranging from 0.29 to 0.65 and averaging 0.41 for same specimens, increasing slightly late in ontogeny; pelvic angle ranging from 50° to 85° and averaging 64°, increasing slightly during growth. Greatest width at tips of ambulacra, well above midheight; cross section here pentagonal, interambulacral areas flat to slightly concave (Plate 3, Figs. 8–12).

Basals three, normally arranged, two regular and one small (azygous), azygous basal quadrate, 3.0 mm long, 3.1 mm wide in medium-sized specimen, regular basals hexagonal, about same length and 4.3 mm wide, basals making up about 40% of pelvis (Plate 3, Figs. 5–7); some secondary deposits extending short distance up interbasal sutures from large round to somewhat triangular stem facet 1.7 mm in diameter, with 0.2 mm lumen in center.

Radials five, relatively long, RD axis less than RB axis at all sizes (Text-Fig. 15), 2 mm less in very large holotype (Plate 3, Fig. 13), RD front nearly straight except on posterior side where distinctly concave against hypodeltoid, large lip at radial origin pointing obliquely adoral.

Regular deltoids four, relatively narrow, elongate hexagonal. Adoral part bulbous, with several thick overlayerings of secondary calcite, middle part constricted, strongly concave in profile with raised ridge alongside adoral end of each spiracular slit, aboral part slightly concave in profile (Plate 1, Fig. 2), ornamented with medium, regularly spaced, growth lines. DR sutures nearly straight, forming 150–160° angle, radials slightly overlap deltoids. Mouth pentagonal to star-shaped, surrounded by regular deltoid and epideltoid lips.

Anal deltoids two, hypodeltoid fairly small, squat pentagonal, easily lost (Plate 3, Figs. 8–11); extends further down theca than adjacent regular deltoids, entire lateral margins border spiracular slits, sutures with radials often moderately curved, adoral edge usually raised in center forming hood over anus (Plate 3, Fig. 16). Epideltoid having small, pentagonal, adoral part bordering mouth and anus on opposite sides, and two long aboral limbs extending down alongside anus and under hypodeltoid, epideltoid limbs infolded to form hydrospire folds below spiracular slit. Anus elliptical with hypodeltoid in place (Plate 3, Fig. 12), about same size as mouth.

Ambulacra five, relatively short and wide, 7.5 mm long and 1.9 mm wide in very large holotype, in shape changing from petaloid to lanceolate during growth, strongly convex in cross section, even with or slightly raised above adjacent plate margins (Plate 3, Figs. 1–7), lancet exposed, making up central 20% in adoral two-thirds of ambulacrum (Text-Fig. 14E). Inner and outer side plates supported by lancet, inner side plates grow laterally as they move up ambulacrum, forming raised abmedial lip around outside of large elliptical brachiolar facets which are abmedial (Plate 3, Fig. 14), 8–9 side plate sets per 3 mm length of ambulacrum, tiny brachiolar pit at end of each food groove near highest point on each side of ambulacrum (Text-Fig. 14F). For each side plate, 3–4 lobes along main food groove plus 3–4 lobes adorally and 2–3 lobes aborally along side food groove (Text-Fig. 14E).

Spiracular slits 10, slightly arcuate, moderately long, extending about two-thirds of ambulacral length, few millimeters of aboral end closed off internally by radial growth beneath lancet, adoral end near narrowest point on deltoid, slits do not quite reach adoral edge of anus in CD interray (Text-Fig. 14B). Hydrospires usually five per ambulacral side (10 measurements), possibly four in few cases, pos-

sibly six in one case, top slit about 0.6 mm deep below deltoid edge adorally, aboral end of this slit sometimes visible near radial lip when ambulacrum damaged or side plates missing, enlarged tube apparently present at inner end of each hydrospire fold.

Ornament consists of medium-strength, widely spaced, growth lines (Plate 1, Fig. 2; Plate 3, Fig. 13) on basals, deltoids, and most of radials; RD front of radials consists of coarse, widely spaced, growth lines (Plate 3, Figs. 7 and 14). Secondary deposits present around stem facet, at radial origin and along edges of ambulacra, and over adoral parts of deltoids (probably filling in adoral ends of spiracular slits).

Measurements of specimens in growth series graphed in Text-Figure 15.

Stem, brachioles, and cover plates unknown.

Studied Specimens. Holotype MCZ 811, paratypes MCZ 812–834 (23 specimens and fragments), and MCZ 835 (17 additional fragments).

Occurrence. Known from the lower Lodgepole Limestone at five localities in southwestern Montana; 20 specimens and fragments from Dry Hollow 20–50 ft (6–15 m) above the base of the Paine Member, the holotype and 14 other specimens and fragments from Milligan Canyon East 12–20 ft (3.7–6 m) above the base, four specimens and fragments from Milligan Canyon 15–20 ft (4.5–6 m) above the base, and single specimens from Sand Creek 23 ft (7 m) above the base and from Little Antelope Creek in the float 20–50 ft (6–15 m) above the base.

Etymology. Named for D. Bradford Macurda, Jr., of The Energists, Houston, who revised this genus and its species in the 1960s.

Discussion. Orophocrinus macurdai is a fairly distinctive species and represents one of the earliest occurrences of the genus. It differs from other similar species, such as *O. orbignyanus* and *O. conicus*, by having a conical shape throughout its growth with length slightly greater than width, vault much greater than pelvis, a moderate pelvic angle, RD less than RB at all sizes, hypodeltoid widely bordering the spiracular slits, convex ambulacra with abmedial brachiole facets, and usually five hydrospires per ambulacral side. *Orophocrinus macurdai* is probably most closely related to *O. orbignyanus* of Belgium and perhaps to *O. conicus* from the Late Kinderhook of the Mississippi Valley; all of these species are nearly the same age. *Orophocrinus macurdai* has only been found in a thin east-west strip of sections near the center of the study area in southwestern Montana (see Text-Fig. 8).

Five additional poorly preserved specimens of *Orophocrinus* also from the lower Lodgepole have a different thecal shape with much longer ambulacra than *O. macurdai* and apparently belong to a species very similar to *O. gracilis* from the Late Kinderhook and Osage of the Mississippi Valley.

OROPHOCRINUS cf. O. GRACILIS (Meek and Worthen), 1870

Plate 3, Figures 17–24;
Text-Figures 14C–D; Table 4

Diagnosis. Theca conoidal, L/W ratio about 1.1, V/P ratio about 1.3, pelvic angle about 83°, RD axis much greater than RB axis, hypodeltoid borders spiracular slits, ambulacra long, convex in cross section, raised above thecal plates, brachiolar facets abmedial to central, 4–5 hydrospires per ambulacral side.

Description. Five poorly preserved and fragmentary specimens available closely resembling this species. Theca conoidal, pelvis broadly conical, sides of pelvis nearly straight, vault parabolic with long ambulacra extending down theca (Text-Fig. 14C; Plate 3, Fig. 22). Smallest apparent specimen 6.8 mm long, largest approximately 19 mm long (basals missing). L/W ratio 1.0 and 1.2 in two nearly complete specimens, V/P ratio ranges from 0.6 to 1.46, pelvic angle averages 83° in three incomplete and crushed specimens. Great-

est width at tips of ambulacra well below midheight, cross section here pentagonal with slightly concave interambulacra.

Basals three, normally arranged, two larger and one smaller (azygous) make up nearly 50% of pelvis; in large specimen azygous basal quadrate 5.2 mm long, approximately 4.5 mm wide, larger basals same length, about 6.2 mm wide. Stem facet large, 2.4 mm in diameter with small central lumen 0.1 mm wide; small secondary deposits up interbasal sutures to produce circular facet.

Radials five, long, RD much greater than RB in all but smallest specimen, nearly 3 mm longer in largest theca, RD front nearly straight, fairly large lip at radial origin pointing laterally (Plate 3, Fig. 22).

Regular deltoids four, relatively narrow, elongate hexagonal. Adoral part with 1–2 concentric growth lines, middle part constricted, concave, aboral part slightly concave in profile, growth lines subdued (Plate 3, Fig. 24). DR sutures nearly straight, form 160° angle, radials appear to overlap deltoids.

Anal deltoids apparently two, missing or poorly preserved on all specimens except smallest where epideltoid present (Plate 3, Fig. 18). Hypodeltoid not seen but probably reaches spiracular slits because epideltoid limbs depressed below thecal surface. Epideltoid has small pentagonal part bordering mouth and anus plus two depressed limbs extending aborally and infolded to form hydrospires. Anus probably elliptical in shape with hypodeltoid present.

Ambulacra five, long and fairly narrow, raised above adjacent thecal plates, linear to lanceolate, moderately convex, lancet exposed in center along much of length (Plate 3, Figs. 23–24). Inner and outer side plates supported by lancet, side plates apparently do not grow laterally, brachiole facets appear to be abmedial or perhaps central (Text-Fig. 14D). Longest ambulacra 11.5 mm long and 2.0 mm wide with about 25 side plate sets, over much of ambulacrum six side plates per 3 mm length; five lobes along main food groove and 1–2 more along adoral edge of side food grooves (Text-Fig. 14D).

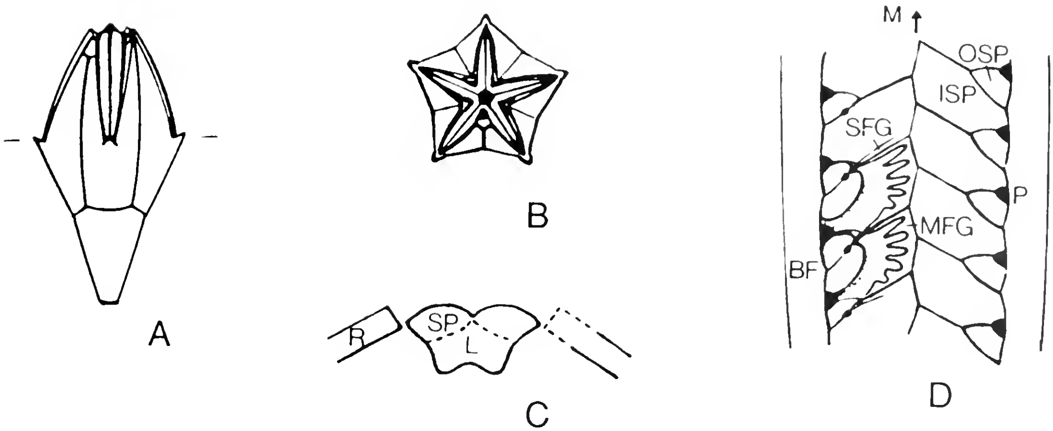
Spiracular slits 10, long, nearly linear, appear to extend most of ambulacral length but aboral 2–3 mm closed off by radial growth beneath lancet, adoral end at narrowest point on deltoids. Either four or five folds per ambulacral side (two observations), folds thin with enlarged tube apparently present at bottom (Plate 3, Fig. 22).

Ornament consists of medium-strength growth lines parallel to plate margins (Plate 3, Fig. 24). Measurements for few known specimens listed in Table 4.

Studied Specimens. MCZ 836–840 (five partial specimens).

Occurrence. Known from the lower Lodgepole Limestone at three localities in southwestern Montana: two specimens from the talus piles at Standard Creek from beds 15–55 ft (4.5–17 m) above the base of the Paine Member, two specimens from Dry Hollow 20–30 ft (6–9 m) above the base, and a single specimen from Little Antelope Creek 26–35 ft (8–11 m) above the base.

Discussion. These five poorly preserved specimens look somewhat different from specimens of *Orophocrinus macurdai*, with which they occur at two localities in Montana. Instead they closely resemble specimens of the distinctive Kinderhook and Osage form *O. gracilis* from the Mississippi Valley (see Macurda, 1965, pp. 1073–1077). The thecal shape and long ambulacra extending down the theca are very similar (compare Plate 3, Figs. 21–22). No hypodeltoid was seen, but it apparently borders the spiracular slits on both sides because the epideltoid limbs are depressed. The basal angle is similar, RD is much greater than RB in all except the smallest specimen (Table 4), the number of hydrospires is similar (four or five vs. four), and the brachiolar facets are in a similar position on the ambulacra. In addition, some specimens from the Mississippi Valley (*O.* cf. *O. gracilis* from the



Text-Figure 16. Morphology of *Metablastus milliganensis*, n. sp. A–B, side and summit views of reconstructed theca based on holotype MCZ 803 and paratype MCZ 804 showing greatest width (short lines) just above midheight and slightly concave interambulacra. C, enlarged cross-sectional view of broken ambulacrum in paratype MCZ 806; note that lancet (L) is "keeled" on the interior, covered externally by side plates (SP), and lacks hydrospires beneath it or the adjacent radials (R). D, much-enlarged plan view of ambulacrum in holotype MCZ 803 showing inner and outer side plates (ISP and OSP) covering lancet, pores (P) at edge of ambulacrum between brachiole facets (BF), and main food groove (MFG) and short side food grooves (SFG) bearing cover plate lobes and sockets. Small arrow points in direction of mouth (M).

Northview Shale of southwest Missouri; see Macurda, 1965, pp. 1075 and 1077) are nearly the same age as the Lodgepole material.

OROPHOCRINUS SP.
Plate 3, Figures 25–27; Text-Figures 14G–I; Table 4

A single coarsely silicified specimen of *Orophocrinus* was found near the top of the Lodgepole Limestone in the southern Bridger Range. The specimen was etched from the slab on which it was collected, and was found to differ from the two *Orophocrinus* species from the lower Lodgepole. However, it is not well enough preserved to establish a new species name for it, but is briefly described and figured here.

Description. Theca conical in shape with rounded vault and conical pelvis; fairly large theca 14.0 mm long, 13.2 mm wide, giving L/W ratio of 1.1; vault 5.1 mm long, pelvis 8.9 mm long, giving V/P ratio of 0.57; pelvic angle about 75° (Plate 3, Fig. 26). Theca pentagonal in summit view with slightly to moderately concave interambulacra, stem facet relatively large. Basals apparently three, fairly large, slightly convex in profile, occupy about 50% of pelvis. Radials five, long, occupy 50% of pelvis and most of vault, RB axis appears greater than RD axis, body slightly concave in profile, little or no radial lip at tip of ambulacra. Regular deltoids four, relatively short, form spiracular slits on margins with ambulacra, moderately concave in cross section. Anal deltoids two, not well preserved, hypodeltoid partly missing but appears to reach spiracular slit on each side, hypodeltoid slightly larger than other deltoid bodies. Ambulacra fairly long, only preserved in two or three rays, lanceolate, appear concave in cross section with raised margins against adjacent radials and deltoids and moderately depressed centers (Plate 3, Figs. 25–26), giving a wide V-shaped cross section (Text-Fig. 14I); lancet partly exposed in center, side plates numerous but not well preserved. Spiracular slits alongside ambulacra, apparently sealed aborally, probably extend half of ambulacral length or less, posterior spiracular slits do not quite reach adoral edge of anus. Summit structures poorly preserved.

Studied Specimen and Occurrence. MCZ 884 from a sequence of thick light beds near the top of the Woodhurst Member of the upper Lodgepole Limestone in the pass just south of Baldy Mountain, southern Bridger Range, southwestern Montana.

Discussion. This specimen with its concave ambulacra appears quite distinct from species of *Orophocrinus* found in the lower Lodgepole and from other previously described *Orophocrinus* species, none of which have flat or slightly concave ambulacra (see Macurda, 1965, table 2). The thecal shape indicates that this specimen is probably related to species such as *Orophocrinus orbignyanus*, *O. conicus*, and *O. macurdai*, n. sp. The concave ambulacra, fairly large stem facet, short spiracular slits, and anal deltoid morphology separate it from all of these species. If other specimens are found and confirm the described morphology, this form will eventually need to be described as a separate species.

Order SPIRACULATA Jaekel, 1918
Family TROOSTRICRINIDAE Bather, 1899
Genus METABLASTUS Etheridge and Carpenter, 1886

Type Species. Pentremites lineatus Shumard, 1858.

Diagnosis. Spiraculate blastoids having an elongate theca (usually biconical); four paired spiracles and a paired anispiracle, anus surrounded by an enlarged hypodeltoid, a smaller adoral superdeltoid, and two hidden cryptodeltoids; 2?–5 hydrospire folds per ambulacral side; ambulacra narrow, lancet completely covered by side plates, one pore per side plate along both radial and deltoid margins; hydrospire plate lacking; deltoids small, strongly overlapped by radials, not appearing on thecal plate surface except for enlarged hypodeltoid; basals sometimes flared with triangular stem facet.

Occurrence. Early to Middle Mississippian; Missouri, Illinois, Iowa, Indiana, Kentucky, and Montana.

Discussion. The discovery of a new *Metablastus* species in Montana extends the range of this genus down to the Kinderhookian. About half the described species have slightly to moderately flared basals with a triangular stem facet, apparently ancestral to the strongly flared basals of the genus *Tricoelocrinus*. The new species of *Metablastus* from Montana has non-flared basals with a round stem facet, and was probably ancestral to other Osagean and Meramecian species with the same feature. *Metablastus* differs from other closely related genera such as *Troosticrinus*, *Tricoelocrinus*, and *Costatoblastus* (see Sprinkle and Gutschick, 1967, p. 391) by having four anal deltoids, regular deltoids not visible in side view, lancet completely covered by the side plates, and a steeply conical to biconical theca without a strongly inflated base, plus its occurrence in the Mississippian.

METABLASTUS MILLIGANENSIS
Sprinkle and Gutschick, new species
Plate 4, Figures 1–13;
Text-Figure 16; Table 4

Diagnosis. Theca biconical, pelvis somewhat longer than vault, basals non-flaring with round stem facet, 2?–3 hydrospires per ambulacral side.

Description. Six partly complete specimens and two separate radial plates available for study; specimens thin-plated and most damaged during acid extraction; description primarily taken from holotype MCZ 803. Thecal shape nearly biconical with slightly expanding conical pelvis and rounded conical vault (Text-Fig. 16A). Holotype 11 mm long, 6.6 mm maximum width (crushed), original width estimated to be 5.5–6.0 mm. L/W ratio now 1.7 (crushed), original L/W ratio probably 1.8–2.0. Vault of holotype 4.6 mm long, pelvis 6.4 mm long, V/P ratio 0.69, probably unaffected by crushing. In two best paratypes, L/W and V/P ratios 1.76 and 0.91, plus 1.82 and 0.76, respectively. Basal angle in holotype now 55–60°, probably closer to 50° in original uncrushed specimen.

Maximum width at base of ambulacra above midheight. Interradial areas slightly concave; ambulacra slightly convex in cross section, only slightly depressed below surface of radials (Text-Fig. 16C). Stem attachment round without flaring basals.

Basals three, normally arranged in a medium-sized cone, making up slightly more than half of pelvis, slightly concave in profile. Two larger and one smaller (azygous) basal; latter in AB interray, 4.0 mm long and 2.5 mm wide; larger basals about same length and about 3.5 mm wide in holotype. Stem facet at tip of cone, nearly round, about 0.8 mm in diameter with a tiny central lumen, secondary deposits very minor around stem facet.

Radials five, elongate, making up most of thecal surface. Each radial has nearly parallel lateral sutures, and most limbs extend nearly to a point at their adoral end. In holotype, radials 7.2 mm long, 2.7 mm maximum width, with body 2.8 mm long and limbs 4.6 mm long along each ambulacrum. Radial body nearly straight in profile, radial limbs slightly curved in profile.

Regular deltoids four, small, not visible on thecal plate surface, strongly overlapped by radials. In holotype, deltoids 0.9 mm long in ambulacral sinus, about 0.2 mm wide, with low crest on summit sloping down to spiracles and deltoid lip. Radiodeltoid suture only slightly raised over ambulacral surface. Spiracles apparently paired, with thin depressed deltoid septum not completely separating spiracles from adjacent ambulacra (Plate 4, Fig. 13).

Anal deltoids poorly exposed or missing from all specimens, should be four in number. Enlarged aboral hypodeltoid exposed on the thecal surface, small adoral superdeltoid, and two hidden cryptodeltoids beneath hypodeltoid. Anispiracle apparently paired also and anus not completely separated from posterior spiracles.

Ambulacra five, narrow, elongate. In holotype, ambulacra about 5.5 mm long, about 0.7–0.8 mm wide along much of length. In separate radials, ambulacral sinus up to 8.0 mm long. Lancet thick, keeled on interior (Text-Fig. 16D), completely covered by side plates, about 10 side plate sets per 3 mm length. Holotype has about 19 side plate sets per ambulacral side, one brachiole facet per side plate set. Sutures between opposing sets of inner side plates in main food groove; small outer side plate notched aboral-abmedial edge of inner side plate (Text-Fig. 16D). One pore per side plate set along radial and short deltoid margins (pores alternate with brachiole facets), short pore furrows indistinct. Side plate sets become smaller (and less oblique) adorally, especially alongside deltoids; side food grooves enter main food groove at 30° angle aborally, nearly 60° angle adorally.

Hydrospires poorly known, apparently at least two and more likely three hydrospires per ambulacral side in paratype MCZ 807. No hydrospire plate present.

Ornament on basals and radials consists of closely spaced growth lines paralleling sutures; best exposed on holotype and nonsilicified separate radials (Plate 4, Figs. 1–2 and 10–11). Secondary deposits nearly lacking from stem facet, only small lip at tip of each ambulacrum at radial origin.

Growth features poorly known because many specimens incompletely preserved; smallest specimen (holotype MCZ 803) 11 mm long, largest specimen (paratype MCZ 806) an estimated 17 mm long (pelvis mostly missing). Measurements for three most complete specimens in Table 4. Stem and brachioles unknown in present material.

Studied Specimens. Holotype MCZ 803, paratypes MCZ 804–810 (five partial specimens and two radial plates).

Occurrence. Known from the lower Lodgepole Limestone at five localities in southwestern Montana: holotype from Antelope Valley 39–45 ft (12–14 m) above the base of the Paine Member, three paratypes from Milligan Canyon East 12–20 ft (3.7–6 m) above the base, one paratype from Milligan Canyon 18–20 ft (5.5–6 m) above the base, one paratype from London Hills about 40 ft (12 m) above the base,

and two radial plates in the float from Northeast Baldy Mountain 20–50 ft (6–15 m) above the base.

Etymology. The species is named for Milligan Canyon, southwestern Montana, where four of the six partial specimens were found.

Discussion. *Metablastus milliganensis* is the seventh species to be described for this genus (see Fay, 1961, pp. 77–82). It can be differentiated from several *Metablastus* species because it does not have flared basals and a triangular stem facet. It differs from the type species *M. lineatus* by being less elongate (much lower L/W ratio), and from *M. bipyramidatus* and *M. varsouviensis* by having the pelvis longer than the vault. At present, *M. milliganensis* is the earliest described species and may have been ancestral to several later species of *Metablastus*, especially *M. lineatus* which occurs in the Burlington Limestone and is the next oldest species.

Family PENTREMITIDAE Orbigny, 1851

Genus MONTANABLASTUS Sprinkle and Gutschick, new genus

Type Species. *Montanablastus baldyensis* Sprinkle and Gutschick, new species.

Diagnosis. Spiraculate blastoids with an obconical theca, vault usually equal to or slightly longer than pelvis; four spiracles and an anispiracle; two or three hydrospires per ambulacral side, two anal deltoids, hypodeltoid enlarged; regular deltoids smaller but appearing on side of theca, form low crests above depressed summit, normal V-shaped radiodeltoid sutures with radials abutting deltoids (no overlap); ambulacra moderately long but fairly narrow, lancet exposed toward adoral end, one pore per side plate along radial and deltoid margins; hydrospire plate apparently absent; plates ornamented with fine growth lines; brachioles about two and a half times the-

PLATE 4

Figures 1–13. *Metablastus milliganensis* Sprinkle and Gutschick, n. sp., lower Paine Member, lower Lodgepole Limestone, 1–3 and 12–13 from Antelope Valley, 4–7 from Milligan Canyon, 8 from London Hills, 9 from Milligan Canyon East, and 10–11 from Northeast Baldy Mountain, southwestern Montana. 1–3, 12–13, A-side, CD-side, top, and E- and B-ambulacral views, respectively, of relatively small holotype MCZ 803 showing shape of nearly complete but crushed theca and morphology of two well-preserved narrow ambulacra, ×2.6 and ×6.5; 4–7, B-side, D-side, top, and bottom views of medium-sized paratype MCZ 804; note shape, missing tip of basals, and concave interambulacra, ×2.6; 8, side view of large paratype MCZ 805 showing large holes in theca and serpulid (left) attached to radials, ×2.6; 9, side view of very large incomplete paratype MCZ 806 still partly in matrix, ×2.6; 10–11, paratype radials MCZ 809 and 810 showing elongate but relatively narrow ambulacral sinuses, ×2.6.

Figures 14–28. *Cryptoblastus*? sp. A, Woodhurst Member, upper Lodgepole Limestone, Sacagawea Peak, Bridger Range, southwestern Montana. 14–15, C-side and top views of relatively small theca MCZ 1049 showing globular shape and eight closely-set spiracles on summit, ×2.7; 16–17, C-side and bottom views of medium-sized theca MCZ 1045; note long ambulacra and concave basal cavity, ×2.7; 18, side view of medium-sized theca USNM 20670 showing elongate shape and rather coarse silicification, ×2.7; 19, partial radial and ambulacrum MCZ 1051; note side plates and radial ornament, ×2.7; 20, large radial, deltoid, and ambulacrum USNM 20670; note short deltoid at upper right, ×2.7; 21–22, B-side and top views of relatively large globular theca MCZ 1046 showing eight closely-set spiracles on summit, ×2.7; 23–24, C-side and bottom views of large elongate theca MCZ 1047; note long ambulacra and small concave basals, ×2.7; 25, interradial side view of large broken theca MCZ 1050 with fine growth lines, ×2.7; 26, side view of large broken theca MCZ 1055 in etched slab showing disrupted plates at top of theca from horizontal worm burrow, ×2.7; 27, side view of very large broken theca MCZ 1048; note growth lines and long ambulacral sinus, ×2.7; 28, top view of eroded theca MCZ 1053 showing summit features and trace of hydrospires beneath C-ambulacrum, ×2.7.

Figures 29–30. *Cryptoblastus*? sp. C, upper Paine Member, middle Lodgepole Limestone, Northeast Baldy Mountain, Bridger Range, southwestern Montana. Side and bottom views of weathered globular theca MCZ 1040 in slab showing eroded slightly convex base, growth lines on radial (30, upper right), and brachioles radiating from all five long ambulacra, ×2.8.

Figures 31–34. *Cryptoblastus*? sp. B, upper Paine Member, middle Lodgepole Limestone, Bandbox Mountain, west-central Montana. 31, surface view of small deltoid MCZ 1041; note closely-set spiracles, two large spines in center, and growth lines aborally, ×6; 32, edge view of small deltoid MCZ 1042 showing three large spines and trace of hydrospire folds, ×6; 33, radial fragment MCZ 1044 with long ambulacral sinus, ×6; 34, basal set MCZ 1043 with parts of D and E radials; note stem facet on slightly convex basals, growth lines, and large lip at each radial origin, ×6.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cal length; small-diameter stem having slightly flanged columnals.

Occurrence. Early Mississippian (Late Kinderhookian) (=Earliest Carboniferous-Tournaisian), Montana.

Etymology. Named for the state of Montana, where this new genus was discovered.

Discussion. Most of the available specimens of this genus are exceptionally well preserved with attached brachioles and stem; unfortunately, as in most blastoid occurrences preserved like this, it is very difficult to identify these specimens and study their thecal morphology. Several specimens with buried appendages were partly silicified, and the appendages were sacrificed to uncover the theca by acid etching. However, this was only partly successful because of incomplete silicification and small size of the specimens. *Montanablastus* resembles several other genera in the Family Pentremitidae, but cannot easily be assigned to any of them. It differs from *Hyperoblastus, Conuloblastus, Devonoblastus*, and *Eleutheroblastus* (all Devonian genera, see Fay and Wanner, 1968) by apparently having only two anal deltoids plus other differences in thecal shape, deltoids, ambulacra, and the later age. It differs from Early Mississippian genera such as *Petaloblastus* (see Fay, 1962a) by having much narrower ambulacra with less lancet exposure and V-shaped radiodeltoid sutures, from *Pentremoblastus* by having narrower ambulacra and only two anal deltoids, and from early species of *Pentremites* by having narrower ambulacra and smaller but crested deltoids. Specimens of *Montanablastus* show considerable resemblance to *Metablastus* and *Costatoblastus* (see Sprinkle and Gutschick, 1967, table 1), but these have paired spiracles, thus belonging in a different family, plus differently shaped deltoids and thecal ornament.

MONTANABLASTUS BALDYENSIS
Sprinkle and Gutschick, new species

Plate 5, Figures 1–8;
Plate 6, Figures 33–43;
Text-Figure 17; Table 4

Diagnosis. Theca obconical, vault usually slightly greater than pelvis; fairly narrow ambulacra, lancet making up only about 25% of ambulacral width; hypodeltoid about one and a half times as long as other deltoid bodies; ornament consists of fine growth lines, large radial prong at tip of ambulacra; columnals slightly flanged.

Description. At least 30 specimens available for study, including holotype MCZ 886, 26 paratypes either etched out from the matrix or on slabs with attached appendages, and several other possible specimens. Theca obconical, pelvis conical, vault truncated conical to parabolic, sum-

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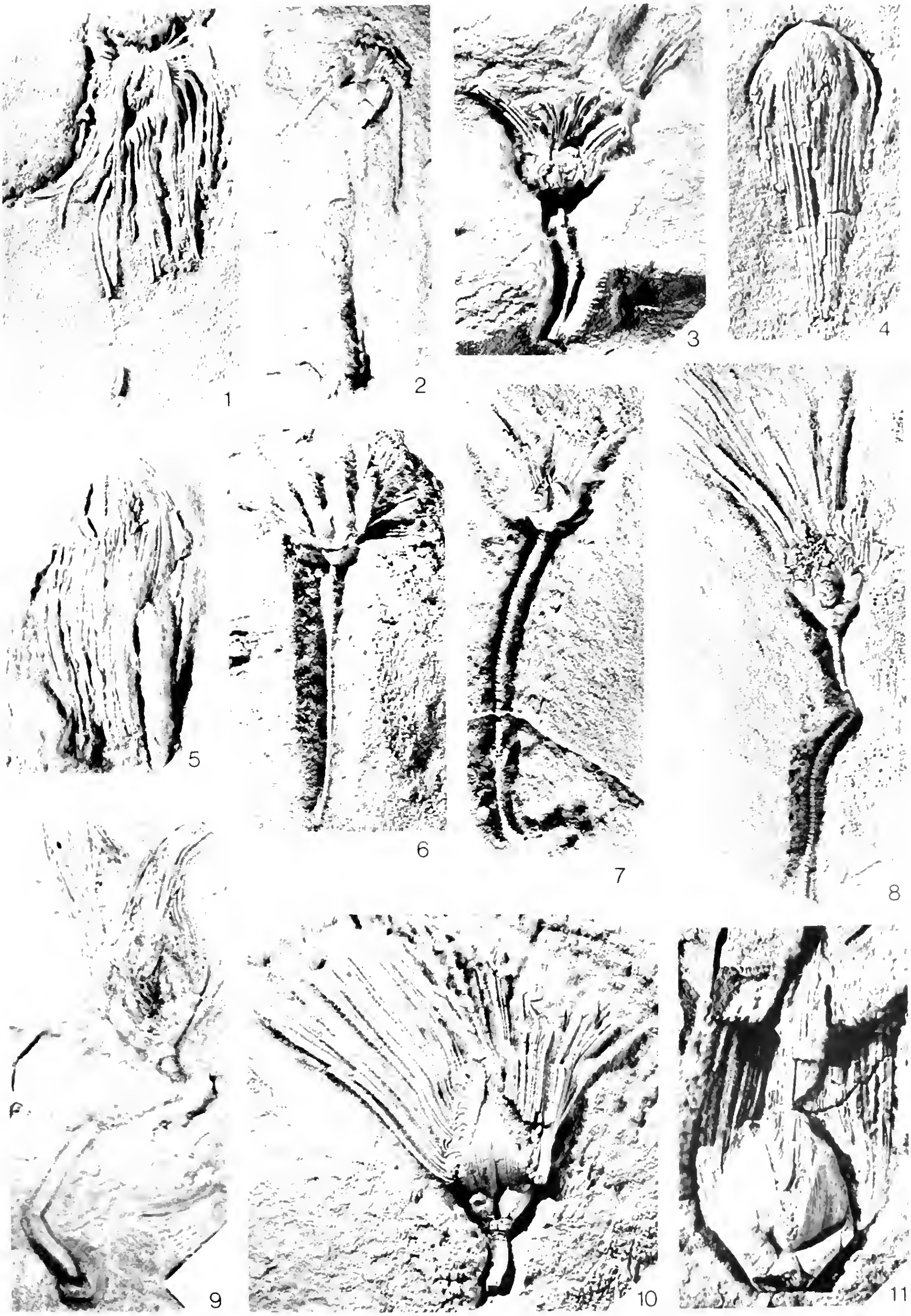
PLATE 5

Figures 1–8. *Montanablastus baldyensis* Sprinkle and Gutschick, n. gen., n. sp., slab specimens from middle Paine Member, middle Lodgepole Limestone, Northeast Baldy Mountain, Bridger Range, southwestern Montana. 1, paratype MCZ 898 showing many long, complete, recurved brachioles, long stem with segment missing, and theca tangled up with Y-shaped ramose bryozoan, ×2; 2, paratype MCZ 903 with crushed theca, few recurved brachioles, and long stem, ×2; 3, paratype MCZ 882 showing many brachioles and deeply-buried stem, ×2; 4, paratype MCZ 900 with tightly-recurved long brachioles hiding most of theca, ×2; 5, paratype MCZ 899 showing long recurved brachioles attached to edges of ambulacra, ×2; 6, paratype MCZ 905 with splayed-out brachioles and deeply-buried stem, ×2; 7, paratype MCZ 901 showing short broken brachioles and long stem with recurved tip, ×2; 8, paratype MCZ 902 with long brachioles and long, deeply-buried, kinked stem emerging from edge of slab (arrow), ×2.

Figures 9–11. *Strongyloblastus laudoni* Sprinkle and Gutschick, n. sp., slab specimens from middle Paine Member, middle Lodgepole Limestone, 9 from Ant Park, Little Belt Mountains, west-central Montana, 10–11 from Northeast Baldy Mountain, Bridger Range, southwestern Montana. 9, paratype MORI 001 (Welch Collection) immersed in water showing badly-crushed theca covered by long brachioles and long, fairly large stem incomplete distally, ×2; 10, paratype MCZ 872 with thecal growth lines, long brachioles attached to edges of ambulacra, and short stem segment, ×2; 11, paratype MCZ 873 showing broken thecal base, small but visible deltoids, and brachioles, ×2.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mit depressed with deltoids projecting above peristome (Text-Fig. 17A). Most specimens fairly small; smallest theca 2.2 mm long, largest theca 10 mm long. L/W ratio ranges from 1.13 to 1.45 and averages 1.32 (10 measurements), gradually increasing with size; V/P ratio ranges from 0.7 to 1.36 and averages 1.02 (eight measurements), showing considerable variation but no obvious trends; and pelvic angle varies from 55° to 75° and averages 69° (eight measurements), gradually increasing with size. Maximum width at large radial lips usually just below midheight; interambulacral areas flat to slightly convex ignoring radial lips, but somewhat concave if radial lips included (Text-Fig. 17B).

Basals three, normally arranged, represent about 50% of pelvis, flat to slightly concave in profile, two larger and one smaller (azygous), azygous basal quadrate, larger basals hexagonal. Stem facet slightly triangular with only small secondary deposits forming platform.

Radials five, large, forming about 50% of pelvis and most of vault, RD axis apparently greater than RB axis at all sizes, large lip up to 0.9 mm long near origin of radials pointing obliquely outward and continuing pelvis profile, lip probably

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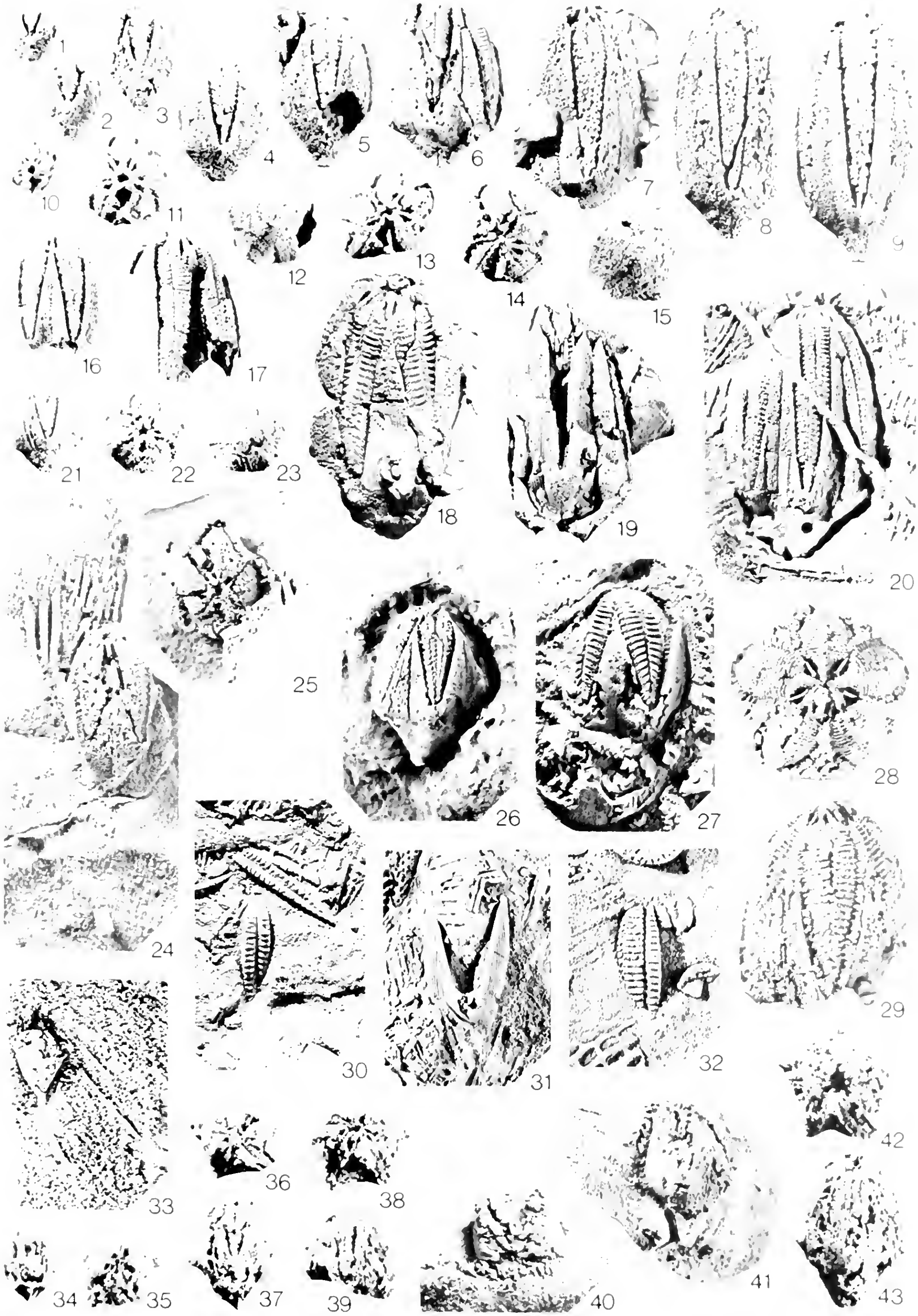
PLATE 6

Figures 1–20. *Strongyloblastus breimeri* Sprinkle and Gutschick, n. sp., lower Paine Member, lower Lodgepole Limestone, 1, 3–5, 9–12, 16, and 19 from Milligan Canyon East, 2, 6, 7, 13, and 17 from Milligan Canyon, 8 and 14–15 from South Boulder, 18 from Dry Hollow, and 20 from Saddle Peak, southwestern Montana. 1, 10, E-side and top views of very small paratype MCZ 843 showing elongate shape, short ambulacra, and separate spiracles, ×2.3; 2, B-side view of small paratype MCZ 844; note vault now longer than pelvis, ×2.3; 3, E-side view of small paratype MCZ 847 showing longer ambulacra and growth lines on radials, ×2.3; 4, 11, D-side and top views of medium paratype MCZ 849; note separate spiracles and damaged base, ×2.3; 5, 12, E-side and bottom views of medium paratype MCZ 851 showing elongate shape and stem facet, ×2.3; 6, B-side view of crushed paratype MCZ 853; note deltoid length and growth lines on radial, ×2.1; 7, C-side view of large paratype MCZ 855 still partly enclosed in matrix, ×2.1; 8, 14–15, D-side, top, and bottom views of large holotype MCZ 841 showing elongate theca with vault much longer than pelvis, separate spiracles on summit, and secondary deposits around stem facet, 2.1; 9, B-side view of very large paratype MCZ 857; note very long, wide ambulacra and deltoid bodies ending well below summit, ×2.1; 13, top view of medium paratype MCZ 860 showing separate spiracles and C-spiracle partly cut off from rest of anispiracle, ×2.3; 16, AB-side view of medium paratype MCZ 862 with rounded summit, ×2.1; 17, C-side view of very large broken paratype MCZ 861 showing enlarged hypodeltoid (top left) and separate spiracles, ×2.1; 18, oblique EA-side view of medium paratype MCZ 854 still partly in matrix; note well-preserved ambulacra showing brachiole facets plus lobes and sockets, and epideltoid (top rear) somewhat larger than other deltoid lips, ×3; 19, side view of large crushed paratype MCZ 866 missing most of the ambulacra but having well-preserved growth lines on the radials, ×2.3; 20, side view of very large crushed paratype MCZ 859 in slab showing long wide ambulacra, visible deltoids, and separate spiracles, ×2.1.

Figures 21–23. *Strongyloblastus* sp., lower Paine Member, lower Lodgepole Limestone, Targhee Peak, southeastern Idaho; A-side, top, and bottom views of small but well-preserved theca MCZ 870 showing different shape from 1–3 above, separate spiracles with C-spiracle cut off from rest of anispiracle (22), and growth lines on radials, ×2.5.

Figures 24–32. *Strongyloblastus laudoni* Sprinkle and Gutschick, n. sp., upper Paine Member, middle Lodgepole Limestone, Northeast Baldy Mountain, Bridger Range, southwestern Montana. 24–25, oblique EA-side and top views of medium paratype MCZ 874 partly etched from matrix; note wide ambulacra, separate spiracles, silicified brachioles from back ambulacra, and stem emerging from matrix (24, bottom), ×3; 26, side view of medium paratype MCZ 875 showing short but visible deltoids and lancet in center of ambulacrum, ×2.9; 27, side view of medium paratype MCZ 878; note well-preserved ambulacra with brachiole facets and pore furrows, ×3; 28–29, top and D-side views of large silicified but broken holotype MCZ 871 showing separate spiracles, thin septum barely cutting off C spiracle from rest of anispiracle, wide ambulacra with brachiole bases still attached to some facets, and cover plates over proximal ambulacra and mouth, ×3; 30, two wide lancet plates (paratype MCZ 881) on a slab, ×3; 31, radial plate (paratype MCZ 879) with wide sinus and well-developed growth lines, ×3; 32, lancet with partial side plates (paratype MCZ 880) showing lancet width and brachiole facets (left), ×3.

Figures 33–43. *Montanablastus baldyensis* Sprinkle and Gutschick, n. gen., n. sp., upper Paine Member, middle Lodgepole Limestone, Northeast Baldy Mountain, Bridger Range, southwestern Montana. 33, very small weathered paratype MCZ 909 in slab; note attached stem segment and two adjacent brachioles, ×3; 34, side view of small silicified paratype MCZ 891 showing exposed plate sutures, ×3; 35, 37, top and C-side views of medium silicified paratype MCZ 889; note four spiracles plus anispiracle (35), plate sutures, and large radial lips, ×3; 36, 39, top and A?-side views of medium paratype MCZ 888 showing deltoids, traces of oral cover plates, and fairly narrow ambulacra, ×3; 38, top view of medium silicified paratype MCZ 887; note four spiracles and epideltoid bordering anispiracle, ×3; 40–41, top and side views of medium silicified paratype MCZ 893 in slab showing thecal shape and many brachiole segments, ×3; 42–43, top and E-side views of fairly large silicified holotype MCZ 886 showing thecal shape, relatively narrow ambulacra, and large radial lips, ×3.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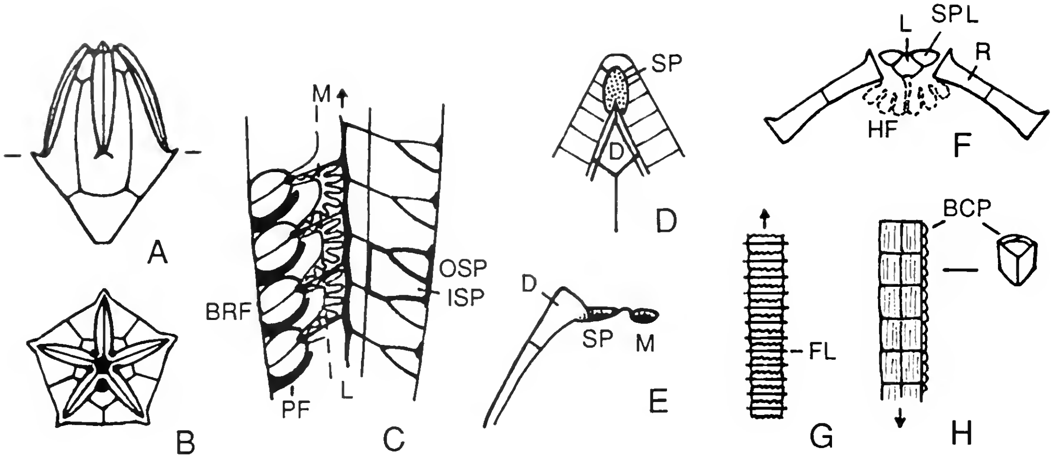


Text-Figure 17. Morphology of *Montanablastus baldyensis*, n. gen., n. sp. A–B, side and summit views of large theca based on paratype MCZ 889 and holotype MCZ 886; note shape, location of maximum width just below midheight (short lines), and summit features. C, much-enlarged plan view of ambulacrum in paratype MCZ 896 showing lancet (L) exposed in center, large inner and small wedge-shaped outer side plates (ISP and OSP) together supporting a hemi-elliptical brachiolar facet (BRF), pore furrow (PF) curving around lower edge of facet, and cover plate lobes and sockets. D–E, much-enlarged plan and side views of spiracle (SP) and mouth (M) on depressed summit with adjacent raised deltoid (D) and adoral ambulacra; based mostly on paratypes MCZ 886 and 887. F, enlarged cross section through adoral theca in paratype MCZ 895 showing ambulacrum made up of lancet (L) and side plates (SPL), adjacent radial limbs (R) with raised edges, and apparently three, poorly preserved, silicified hydrospire folds (HF) on each side, ×8.6. G, proximal stem in paratype MCZ 898 showing columnal shape and thin flange (FL) around center; arrow points to attachment at base of theca, ×17.2. H, side view and cross section of brachiole in paratypes MCZ 898 and 905; note striations on side and low biserial set of cover plates (BCP) over relatively deep, V-shaped, food groove; arrow points to attachment on ambulacrum, ×21.5.

formed from secondary deposits, but one theca has lip with closely spaced growth lines.

Regular deltoids four, small, body triangular, extends only short distance down thecal surface but visible in side view, V-shaped suture between radials and deltoid forming 80–85° angle, deltoids slightly concave in profile, radials abut deltoids without obvious overlap. In several thecae, deltoids 0.8–0.9 mm long, projecting above nearly flat summit (Plate 6, Figs. 36–39), sharp adoral edge of deltoids dropping away rapidly to below summit level; four spiracles formed in front of projecting deltoid bodies by edges of ambulacra and curved deltoid lips, spiracles teardrop-shaped, small, with depressed deltoid septum not reaching surface (Text-Figs. 17D–E).

Anal deltoids apparently two, somewhat enlarged hypodeltoid aborally, 1.2–1.5 mm long (about one and a half times length of regular deltoids), slightly ridged with stronger growth lines; epideltoid small, separates mouth from anispiracle, depressed aboral side has three troughs for central anus and two lateral hydrospire groups (Plate 6, Fig. 38), septa separating these troughs depressed to form true anispiracle, no evidence of cryptodeltoids.

Ambulacra five, moderately long, fairly narrow, slightly convex in cross section, lancet partly exposed in center of adoral half, forming about 25% of ambulacral width, side plates on bevelled abmedial edges of lancet, appear to be normally arranged but not well preserved or exposed in most specimens, 14 side plate sets present in one ambulacrum 4.0 mm long, side food grooves meet main food groove at 45–60° angle, inner side plates apparently large, rectangular, outer side plates not obvious but probably small triangular wedges underlying half of brachiole facets, brachiole facets large, at slight angle to side

food grooves, occupy about half of ambulacral width (Text-Fig. 17C). Main food groove has 4–5 lobes between each pair of side food grooves, which have about three smaller lobes on the adoral and aboral sides.

Hydrospires in 10 groups, apparently 2–3 folds per ambulacral side based on two poorly preserved silicified specimens and a sectioned slab specimen (Text-Fig. 17F).

Ornament consists of fine growth lines on basals and radials, somewhat coarser growth lines on deltoids, hypodeltoid and radial-hypodeltoid growth front.

Nearly two-thirds of specimens have brachioles preserved and nearly half have proximal stem attached; complete brachioles about 15–16 mm long in 6 mm long theca (Plate 5, Fig. 1) with rounded triangular cross section, biserial brachiolar plates (BP), and one low set of tiny biserial cover plates (BCP) often pyritized along with wide V-shaped brachiolar food groove (Text-Fig. 17H). Brachiolar plates about 0.2 mm long, 0.25 mm wide, with a very small central ridge and fine striations extending down length (Text-Fig. 17H); about two BCP/BP where observable. Stems incomplete, ranging up to 29 mm long (attached to theca 5.5 mm long; Plate 5, Fig. 7); this stem has about 190 columnals in this length. Columnals having rounded edges and small equatorial flange, a tiny central lumen, and averaging 0.14–0.15 mm long, 0.5 mm wide proximally, and 0.3 mm (or 0.35 mm with flanges) wide distally (Text-Fig. 17G).

Growth information for the few measurable specimens summarized in Table 4.

Studied Specimens. Holotype MCZ 886, paratypes MCZ 882, 887–913, additional specimens MCZ 914.

Occurrence. All described specimens come from the Northeast Baldy Mountain locality in the southern Bridger Range of southwestern Montana. Specimens occur in series of beds with 6–8 in. (0.15–0.20 m) of limestone interbedded with shaly dolomite from the middle Paine Member between 150 and 175 ft (46–53 m) above the base of this member.

Etymology. Named for the Northeast Baldy Mountain locality where all the studied specimens were collected.

Discussion. *Montanablastus baldyensis* is an unusual blastoid for the Early Mississippian. The fairly narrow ambulacra are not particularly similar to other forms in the Family Pentremitidae; even species such as *Pentremites conoideus* have wider ambulacra with more lancet exposure. The radial lips are very large for a blastoid, continue the profile from the pelvis, and the lip on one specimen shows apparent growth lines, indicating that the lips were produced by periodic small increments of growth and not by secondary deposits. Many specimens with appendages are excellently preserved and were cleaned with an air abrasive unit, but are almost useless for trying to work out the thecal morphology of this species. More and better silicified materials will be necessary before more complete information can be obtained.

Family PENTREMITIDAE? Orbigny, 1851
Genus STRONGYLOBLASTUS Fay, 1962b

Type Species. *Strongyloblastus petalus* Fay, 1962b.

Diagnosis. Spiraculate blastoids with an ovoid, ellipsoidal, or obconical theca; eight divided spiracles plus variable arrangement on anal side (anispiracle, "C" spiracle plus half-paired anispiracle, or "C" and "D" spiracles plus anus); 3–5 hydrospire folds per ambulacral side; two anal deltoids, prominent epideltoid often larger and higher than other deltoid lips, and hypodeltoid with slightly enlarged body and adorally projecting septum more prominent than those of other deltoids; regular deltoids appear on side of theca, deltoid body short to moderately long, sometimes heavily ridged, radials overlap deltoids; ambulacra medium to long, very wide, lancet completely exposed, occupying 40–60% of ambulacral width, one pore per side plate along radials, pores either present along deltoids or closed off short distance above radiodeltoid suture, no hy-

drospire plate present; ornament consisting of fine to coarse growth lines.

Occurrence. Early to Middle Mississippian (Early Carboniferous), southern Canadian Rockies, northern U.S. Rockies, Mississippi Valley, and Alaska.

Discussion. Two new species of *Strongyloblastus* occur in the Lodgepole Limestone in southwestern Montana, one in the lower Paine Member and the second in the upper Paine Member. A single additional specimen from the lower Paine Member is unassigned at present. A third new species belonging either to *Strongyloblastus* or to *Pentremites* (as presently defined) occurs in the younger Castle Reef Dolomite in the Sun River Canyon area of northwestern Montana; this form will be described in a separate paper.

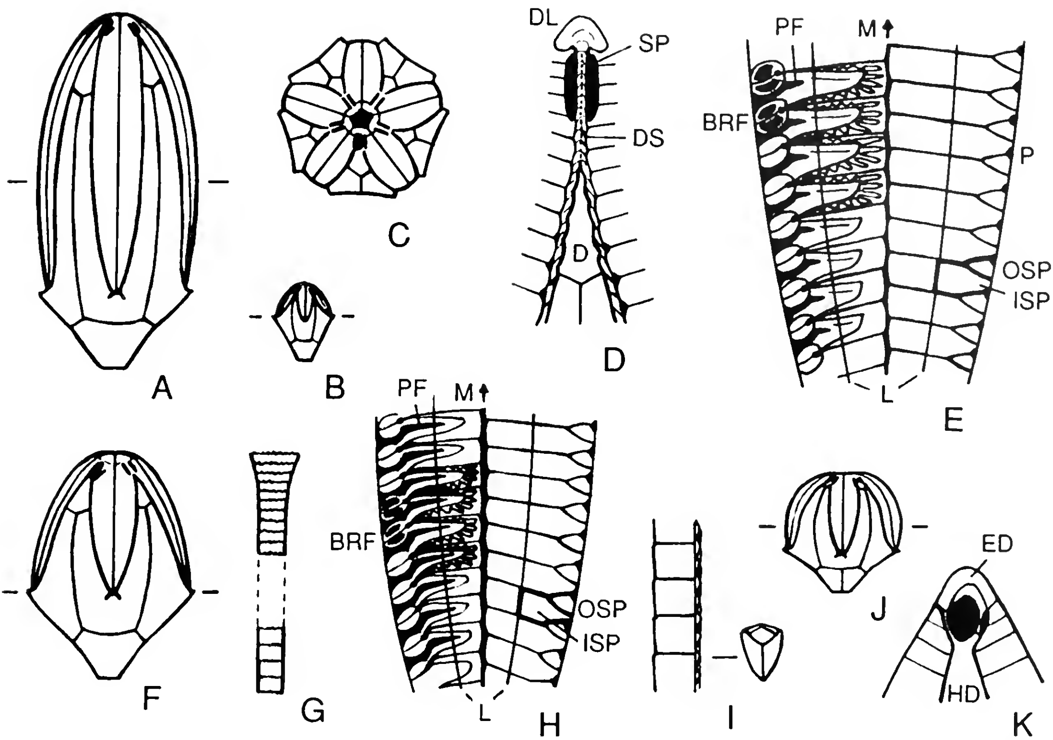
Strongyloblastus was described by Fay (1962b) as a Devonian blastoid from western New York State, based on the label that accompanied the holotype specimen. Macurda and Breimer (1977, p. 693) reported that "*Strongyloblastus* was completely anomalous when compared with other Devonian blastoids," and that similar specimens occur in the Banff Formation of Early Mississippian (probably Late Kinderhookian) age in the southern Canadian Rockies, and concluded that the label with the holotype was incorrect. Occurrences of similar blastoids belonging to different species are known from the northern U.S. Rockies (see following) and from Alaska. Fay (1964) assigned *Strongyloblastus* to the Family Schizoblastidae, but Macurda and Breimer (1977, p. 694) assigned it to the Family Pentremitidae after some discussion because of its overall resemblance to several early species of *Pentremites*, although this family then cannot be characterized alone by having four spiracles and an undivided anispiracle.

Strongyloblastus is most closely related to several early species of *Pentremites* with divided spiracles, such as *P. elongatus* and *P. kirki* (Macurda, 1975; Horowitz, Waters, and Macurda, 1981; Horowitz, Macurda, and Waters, 1986). *Strongyloblastus* differs only slightly from *Pentremites* species having divided spiracles (see Macurda and Breimer, 1977, p. 696) by having nonfunctional ambulacral pores along most of the deltoid margin and higher septa separating the anus from one or both of the posterior spiracles. These differences are very minor and intermediate stages occur in some of the new species described here, in contrast to the difference between divided and undivided spiracles, a difference that previously would have placed these blastoids in different families (see Fay, 1964; Fay and Wanner, 1968).

Instead of having these two genera separated by such minor differences at present, we propose that all species with divided spiracles now assigned to or inferred to belong to *Pentremites* (*P. elongatus, P. kirki*, and one or more undescribed species from Montana, western Canada, and Alaska) be assigned to the genus *Strongyloblastus* Fay (1962b). This proposed change would restrict *Pentremites* to species having undivided spiracles (like its type species *P. godoni*), remove two named and described species from the genus, and restrict its range to Middle Mississippian (Meramecian) to Early Pennsylvanian (Morrowan). *Strongyloblastus* would range throughout much of the Early Mississippian from the late Kinderhookian in the Rocky Mountains (Lodgepole Limestone, Banff Formation) to at least the late Osagean in the Midwest (Burlington Limestone) and perhaps higher in the Rocky Mountains. *Strongyloblastus* may have been ancestral to *Pentremites* by suppression of the deltoid septa in the regular spiracles and anispiracle, retention of functional pores along the deltoid margins, and perhaps enlargement of the deltoid body.

STRONGYLOBLASTUS BREIMERI
Sprinkle and Gutschick, new species
Plate 1, Figures 4–5;
Plate 6, Figures 1–20;
Text-Figures 18A–E and 19

Diagnosis. Theca changing from obconical to elongate ellipsoidal during growth, L/W ratio averages 1.61, V/P ratio av-



Text-Figure 18. Morphology of *Strongyloblastus breimeri*, n. sp. (A–E), *S. laudoni*, n. sp. (F–I), and *S.* sp. (J–K). A–C, enlarged side views of large paratype theca MCZ 857 and small paratype theca MCZ 843 and summit view of large theca showing considerable change in shape between biconical juvenile and ellipsoidal adult, very long and wide ambulacra, separate spiracles and half-paired anispiracle on summit, and short lines at maximum width. D, much-enlarged deltoid body (D), thin deltoid septum (DS) separating elliptical spiracles (SP), and deltoid lip (DL) separating spiracles from mouth in paratype MCZ 854, ×8.6. E, plan view of ambulacrum in MCZ 854 showing wide exposure of lancet (L) in center, large inner and small triangular outer side plates (ISP and OSP) supporting a brachiole facet (BRF) at the ambulacral edge, curved pore furrow (PF) extending from pore (P) toward center of ambulacrum, and numerous cover plate lobes and sockets, ×14.6. F, side view of paratype theca MCZ 875 showing different shape and shorter ambulacra from A above (maximum width at short lines), ×2.1. G, proximal and medial stem in MORI 001; note enlarged proximal stem with thin columnals just below attachment and lack of flanges on columnals, ×3.4. H, plan view of ambulacrum in MCZ 878 showing lancet (L) exposed in center, inner and outer side plates (ISP and OSP), brachiole facets (BRF) at ends of side food grooves, and somewhat longer pore furrows (PF) just reaching lancet, ×3.9. I, much-enlarged side view and cross section of brachiole in MCZ 872; note smooth brachiolar plates and cover plates over shallow food groove, ×12. J, side view of small theca MCZ 870 showing difference in shape from B above (short lines at maximum width), ×3.2. K, enlargement of anal side in MCZ 870 showing epideltoid (ED) septum cutting off C spiracle from rest of anispiracle and reaching hypodeltoid (HD), ×7.6.

erages 2.29, pelvic angle averages 82°, interambulacra slightly concave; ambulacra long, moderately to strongly convex, lancet fully exposed, occupying about 50% of ambulacral width; one pore per side plate set along radials, pores absent just above radiodeltoid suture because of ridges on edge of deltoid; eight spiracles and a half-paired anispiracle on summit, one epideltoid limb partly separates "C" spiracle, "D" spiracle and anus not separated; deltoids fairly long but body on thecal surface short except for enlarged hypodeltoid, surface of deltoids not ridged; three hydrospire folds per ambulacral side.

Description. Forty-seven specimens and fragments available for study; description based on holotype MCZ 841, 17 additional nearly complete paratypes in growth series, and 10 other specimens and fragments. Theca obconical in small specimens changing to ellipsoidal in medium to large

ones (Text-Figs. 18A–B); in adults, theca made up mostly of long parabolic vault with a short conical pelvis. Growth series specimens range from 3.9 mm long to 22.9 mm long, holotype a large, slightly compressed theca 18.6 mm long (Plate 6, Figs. 8, 14–15). In 18-specimen growth series, L/W ratio ranges from 1.30 to 2.24 and averages 1.61, increasing gradually above a length of 15 mm; V/P ratio ranges from 0.96 to 3.88 and averages 2.29, increasing dramatically throughout growth; and pelvic angle ranges from 65° to 95° and averages 82°, increasing in small specimens up to about 9 mm long. Greatest width near midheight in large specimens, at or just above tips of ambulacra in small thecae (Text-Figs. 18A–B). Pelvis profile slightly concave, interambulacra slightly concave near midheight, ambulacra moderately to strongly convex all along length, edges slightly depressed below adjacent thecal plate surfaces.

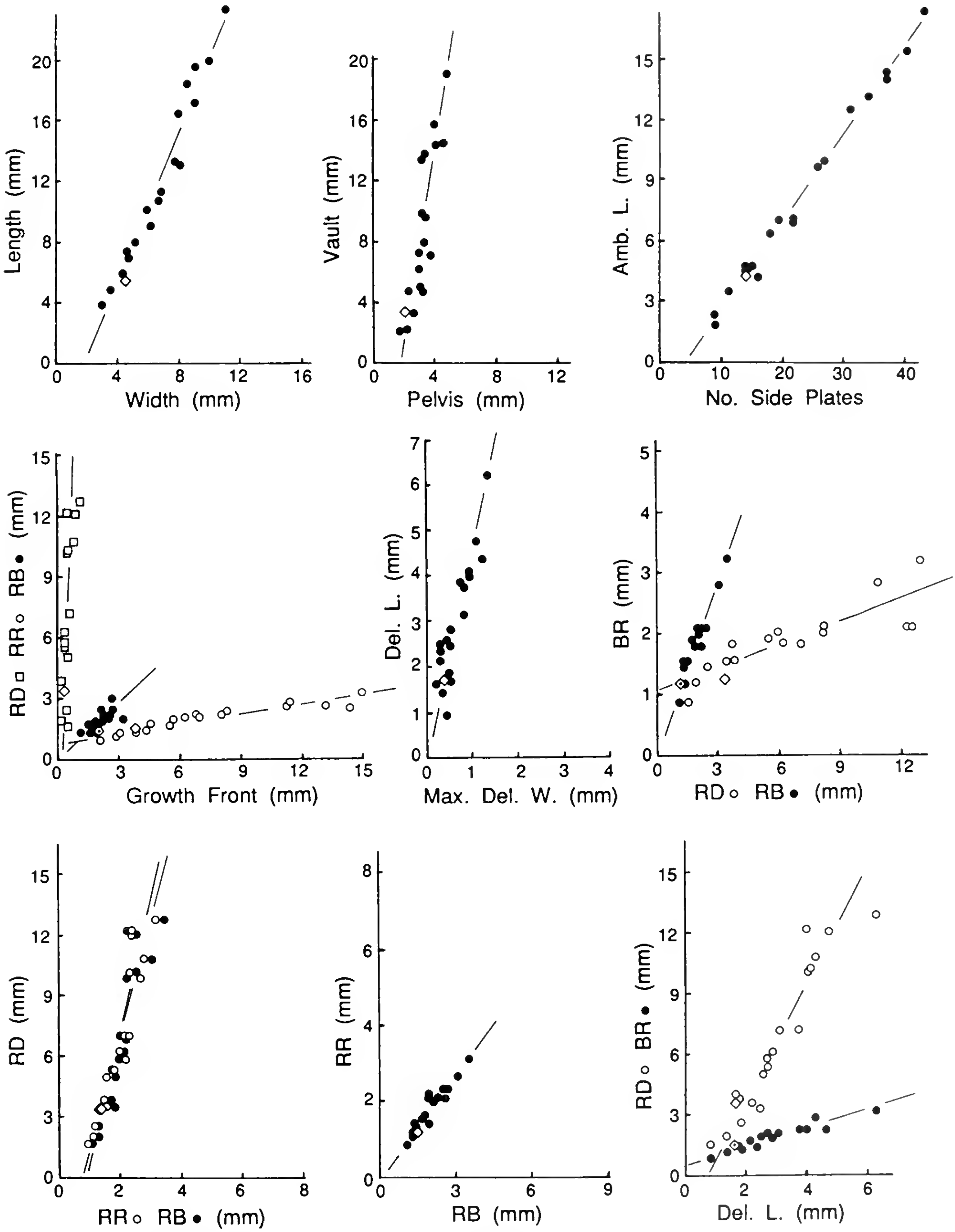
Basals three, normally arranged, forming about half of pelvis; two larger, one smaller (azygous), azygous basal quadrate, 2.4 mm long and 1.9 mm wide in medium-sized specimen; larger basals hexagonal, about same length, approximately 2.9 mm wide (somewhat distorted); stem facet relatively large, up to 1.7 mm in diameter with slight ridge around periphery and small central lumen about 0.2 mm in diameter, facet on raised platform of secondary deposits covering origin of basals.

Radials five, very long, making up most of thecal surface, RD axis slightly greater than RB axis in smallest specimens, many times greater in largest ones (Text-Fig. 19), RD and RHD fronts nearly straight, radials overlap deltoids along short suture, radial limbs raised along ambulacral margins (slight secondary deposits on surface) but edges not grooved here, small wide lip at radial origin pointing laterally.

Regular deltoids four, body short and narrow, above level of adjacent ambulacra, septum and lip long and narrow, at or just above level of ambulacra (Text-Fig. 18D). Deltoid lip triangular, notched by spiracles aborally; septum long, about 0.4 mm wide, relatively sharp, separates spiracles and adjacent ambulacra, grooved on edges facing spiracles; deltoid body triangular, flat to slightly concave, nearly smooth on surface, edges grooved at each brachiole facet on ambulacrum (Text-Fig. 18D), with a slightly M-shaped DR suture making an angle ranging from 60° to 140° in different specimens; radials strongly overlap deltoids at surface but suture becomes nearly vertical at level of ambulacra. In paratype MCZ 854 (Plate 6, Fig. 18), total deltoid length 4.2 mm with body 1.6 mm long and 0.7 mm wide, septum about 1.8 mm long and 0.35 mm wide between spiracles, and lip 0.8 mm long and 1.0 mm wide.

Anal deltoids two, slightly enlarged epideltoid adorally and enlarged hypodeltoid aborally. Epideltoid triangular to inverted U-shaped, slightly wider than other deltoid lips, extends higher above mouth, notched aborally by "C" spiracle (cut off by low epideltoid septum) and half-paired anispiracle (Plate 1, Fig. 5). Hypodeltoid enlarged over other deltoids, body extends about 1 mm further down theca in several large specimens, nearly 1.6 times size of other deltoids in one fragment (4.2 vs. 2.6 mm; Plate 6, Fig. 17), hypodeltoid septum wider and higher than other deltoid septa, extending up to form raised hood over aboral edge of half-paired anispiracle (Plate 1, Fig. 5), right edge meets raised septum from epideltoid cutting off "C" spiracle. Half-paired anispiracle slightly asymmetric, elliptical, slightly larger than mouth; "C" spiracle elongate, slightly smaller than other spiracles.

Ambulacra five, long, very wide, strongly convex aborally to moderately convex adorally, about 15 mm long in holotype, about 2.5 mm wide at widest point; lancet completely exposed in center, occupies about 50% of ambulacral width, fairly thin in cross section; side plates on bevelled edge of lancet, inner side plates medium-sized, wide, nearly rectangular, outer side plate small, triangular, on aboral-abmedial edge



Text-Figure 19. Growth plots for 19 measured specimens (MCZ 841–859) of *Strongyloblastus breimeri*, n. sp., plus single small specimen (MCZ 870) of *S.* sp. (white or dotted diamond). Note large size range and nearly equal RR and RB growth vs. much faster RD growth. Best-fit lines in all plots were hand fit.

of inner side plates, each side plate set forms one brachiole facet at edge of ambulacrum (Text-Fig. 18E). Main food groove extending down center of each ambulacrum, between side food grooves having about four lobes on each side formed by lancet; side food grooves long, empty into main food groove at 50–85° angle, each has 5–6 lobes on adoral side, 3–4 cryptic lobes aborally (formed by lancet and inner side plate), large brachiolar pit at end of side food groove; brachiole facets well developed, elliptical, tilted about 30–40° to side food groove, closely spaced, made up of two shallow depressions. One pore per side plate set along radials, alternating with brachiole facets along smooth radial edge, short to medium-length pore furrow extending in from pore between brachiole facets almost to lancet; pores apparently absent from deltoid margin just above radiodeltoid suture because deltoid edge grooved (at each brachiole facet) and vertical deltoid ridge between grooves extends into apparent pore position at edge of ambulacrum.

Hydrospire groups 10, extend short distance into coelomic cavity from ambulacrum sides, three hydrospires per group (poorly preserved in three specimens), short slit and enlarged tube at bottom of each hydrospire, no hydrospire plate present.

Ornament consists of medium to strong growth lines parallel to plate sutures on basals and radials, fine growth lines on deltoids (Plate 6, Figs. 19–20), chevrons on radial limbs below enlarged hypodeltoid somewhat coarser than other growth lines, deltoids not coarsely ridged so far as known.

Measurements of specimens in growth series plotted in Text-Figure 19.

Stem, brachioles, and cover plates unknown.

Studied Specimens. Holotype MCZ 841, paratypes MCZ 842–868 (27 specimens and fragments), and MCZ 869 (19 additional partial specimens and fragments).

Occurrence. Known from the lower Lodgepole Limestone at six localities in southwestern Montana; 21 specimens from Milligan Canyon East 12–20 ft (3.7–6 m) above the base of the Paine Member, 20 specimens and fragments from Milligan Canyon 20–25 ft (6–7.5 m) above the base, the holotype and one other specimen from South Boulder Canyon in the float from beds about 40 ft (12 m) above the base, and single specimens from Dry Hollow 30–35 ft (9–11 m) above the base, from the talus piles at Standard Creek from beds 15–54 ft (4.5–16.5 m) above the base, and from Saddle Peak 55–60 ft (17–18 m) above the base.

Etymology. Named for Albert Breimer, State Museum of Geology and Mineralogy, Leiden, Netherlands, one of the authors who restudied the type species *Strongyloblastus petalus* and corrected its age and occurrence and re-evaluated its phylogenetic position.

Discussion. Strongyloblastus breimeri is somewhat intermediate in its morphology between *S. petalus*, the type species, and "*Pentremites*" *elongatus*, perhaps an argument for assigning all three of these species to the same genus. It resembles *S. petalus* by having a half-paired anispiracle (see below), the epideltoid and hypodeltoid raised and somewhat enlarged, by having the pores closed off along much of the deltoid margin, by having smooth radial edges vs. ridged deltoid edges, and by being almost the same age (Late Kinderhookian). It resembles "*P.*" *elongatus* in its general theca shape, by having three hydrospire folds per ambulacral side, by having nearly smooth deltoid bodies, and by having the hypodeltoid somewhat enlarged over the regular deltoids. It differs from both of these species by having a somewhat different thecal shape, much shorter deltoid bodies, and the "C" spiracle just barely separated from the half-paired anispiracle.

An excellently preserved vault of *S. petalus* from the Spreng Collection, University of Missouri, Rolla (UMR 6967; Plate 1, Figs. 6–7), shows the anispiracle and summit better than any of the specimens figured by Macurda and Breimer (1977,

plate 1). It definitely has a half-paired anispiracle similar to but more strongly developed than in *S. breimeri*, with the epideltoid limb separating the "C" spiracle much wider and somewhat higher (Plate 1, Fig. 7). Apparently the epideltoid limbs have variable development in *S. petalus*, with some specimens having a half-paired anispiracle and others having an anus and two separate spiracles on the posterior side. In the Spreng Collection specimen of *S. petalus*, the epideltoid is horseshoe-shaped, much larger and higher than the regular deltoid lips, and produces a mouth that is much wider than high, plus four ambulacra ("B"–"E") that are curved on the summit (Plate 1, Fig. 7), both rather unusual features for a blastoid.

The critical specimen of *S. breimeri* for showing the half-paired anispiracle was taken out of the acetic acid bath at the Indiana University Field Station in southwestern Montana just after the summit and adoral ambulacra were exposed (see Plate 1, Fig. 5), and brought back to Harvard University to be photographed. After being coated with Glyptal, it was put in acid again to extract the rest of the specimen from the matrix; unfortunately, nearly all the earlier summit detail was destroyed by later acid etching (see Plate 6, Fig. 11). Later specimens from the Milligan Canyon localities showing excellent detail during acid etching were removed permanently, even if incompletely exposed.

STRONGYLOBLASTUS LAUDONI
Sprinkle and Gutschick, new species
Plate 1, Figure 3; Plate 5, Figures 9–11; Plate 6, Figures 24–29; Text-Figures 18F–I and 20

Diagnosis. Theca obconical, L/W ratio averages 1.46, V/P ratio averages 1.25, pelvic angle averages 73°, interambulacra flat to slightly convex; ambulacra moderately long, very wide, slightly to moderately convex, lancet fully exposed, occupying 40–50% of ambulacral width; one pore per side plate along radials, pores apparently filled in just above radiodeltoid suture; deltoid body relatively short, crest long, usually depressed below edges of adjacent ambulacra, eight spiracles and a half-paired anispiracle on summit, "C" spiracles barely split off from anispiracle, hypodeltoid not enlarged; three? hydrospire folds per ambulacral side.

Description. Approximately nine specimens and 14 plates available for study, including partly complete, etched holotype MCZ 871, four paratypes in slabs with brachioles and (in three cases) stems preserved, four paratypes in slabs without appendages, and three separate plate paratypes. Theca obconical, changing only slightly in shape during growth through preserved size range, made up of moderately long parabolic vault and moderately short conical pelvis (Text-Fig. 18F). Complete specimens range from about 5.0 mm long to about 14.5 mm long. Holotype a large, well-preserved, incomplete theca etched from slab; as preserved, about 12.0 mm long with complete vault 9.8 mm long and upper part of broken pelvis; original length estimated at 15–16 mm (Plate 6, Fig. 29). Greatest width 9.5 mm just above radial lips, just below apparent midpoint of theca. Interambulacra here flat to slightly convex. In six measurable specimens, L/W ratio ranges from 1.09 to 1.86, averaging 1.46; V/P ratio ranges from 1.25 to 2.11 and averages 1.56; and pelvic angle ranges from 60° to 80°, averaging 73°. Pelvis profile slightly concave, ambulacra slightly to moderately convex.

Basals three, normally arranged, incompletely exposed (or missing) in most specimens, forming about 50% of pelvis, two larger, one smaller (azygous), regular basals hexagonal, about 3.6 mm long and at least 3.5 mm wide in a large specimen; stem facet in this specimen about 1.4 mm in diameter with secondary deposits forming rounded to slightly triangular platform for stem attachment.

Radials five, long, making up most of thecal surface, RD axis greater than RB axis in all available specimens, many times greater in large specimens (Text-Fig. 20),

RD front nearly straight, relatively short; small wide lip at radial origin pointing laterally.

Regular deltoids four, body short to medium in length, fairly narrow in most specimens, septum and lip long and narrow, in some specimens septum below level of ambulacra so that side plates from adjacent ambulacra in contact (Plate 6, Fig. 28). Deltoid body 2.5–3.3 mm long, 1.0–1.8 mm wide in large specimens, much smaller in small specimens; septum and lip at least 2.5 mm long, just barely splitting spiracles at surface of summit, septum sharp-crested, part above surface of ambulacrum somewhat ridged, radiodeltoid suture makes angle between 90° and 120° in different specimens, radials moderately overlap deltoids with about 60° angle from plate surface.

Anal deltoids two, hypodeltoid apparently not enlarged over other deltoids. Epideltoid triangular, slightly wider than other deltoid lips, sends thin septum aborally to cut off "C" spiracle from rest of half-paired anispiracle, anus and "D" spiracle apparently not separated (Plate 6, Fig. 28). Hypodeltoid relatively long, body similar to other deltoids but septum higher and not depressed below adjacent ambulacra, may project slightly at aboral edge of anispiracle, which is elliptical except for slightly flattened side along "C" spiracle septum. "C" spiracle similar in size and shape to other spiracles.

Ambulacra five, moderately long, very wide, slightly to moderately convex in cross section, in holotype, about 10.5 mm long, 3.3. mm maximum width; lancet completely exposed in center, occupies between 40 and 50% of ambulacral width, about 0.3–0.5 mm thick in several ambulacral fragments, side plates abutting edge of lancet, suture nearly vertical everywhere except near aboral end of ambulacrum where lancet somewhat bevelled, inner side plates medium-sized, wide, nearly rectangular, outer side plates small, rounded triangular, located on aboral-abmedial edge of inner side plates, each side plate set forming one brachiole facet at edge of ambulacrum (Text-Fig. 18H).

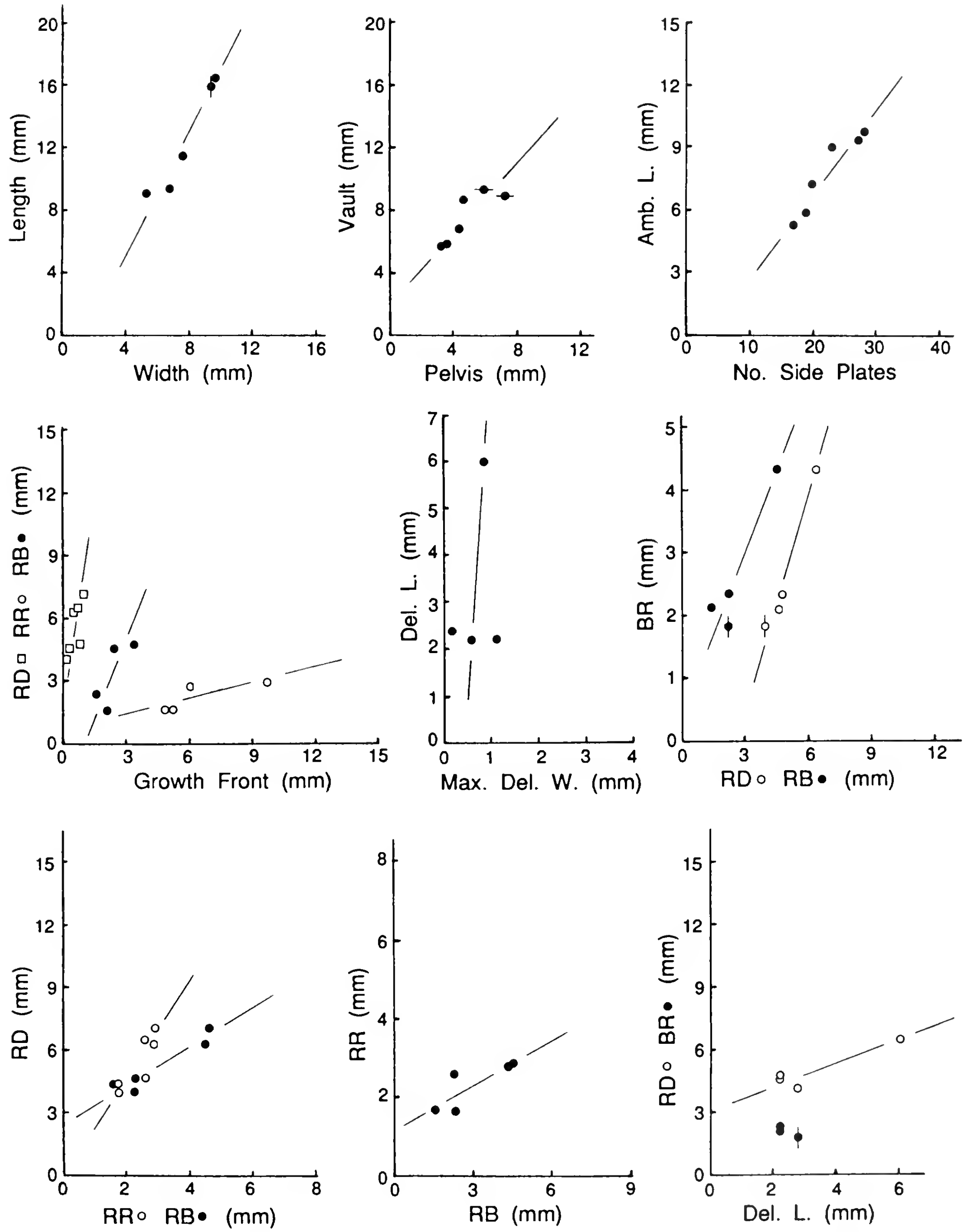
Main food groove extending down center of each ambulacrum, between side food grooves having about 3–5 lobes on each side formed by lancet; side food grooves long, empty into main food groove at 45° angle aborally to 80° angle adorally, each having 8–11 lobes on adoral side, 7–9 smaller lobes on aboral side, both formed by lancet and inner side plates, each side food groove leading to large brachiolar pit about 0.3 mm from edge of ambulacrum and two shallow depressions making up brachiole facet about 0.4 mm long and 0.25 mm wide, turned at 20–30° angle to side food groove, and slanted abmedially and adorally (Text-Fig. 18H; Plate 1, Fig. 3); edge of radial smooth, edge of deltoid body somewhat ridged, one pore per side plate along radials, alternating with brachiole facets; pores apparently absent along deltoid margin just above radiodeltoid suture, because deltoid edge grooved at each brachiole facet and ridges between grooves extend into apparent pore positions at edge of ambulacrum. Pore furrows well developed, arcuate, extending around lower edge of braciole facet, then laterally along raised center of inner side plate and often reaching lancet, pore furrows present along both radial and deltoid margins.

Hydrospire groups 10, poorly known, apparently three hydrospires per group below each ambulacral side.

Measurements for few complete specimens without appendages plotted in Text-Figure 20.

Ornament consists of fine to medium growth lines on basals and radials (Plate 1, Fig. 3), somewhat coarser growth lines on deltoids and along RHD growth front.

Brachioles preserved in at least four specimens, at least 21 mm long in largest example, tightly packed along edge of ambulacrum where attached (Plate 5, Figs. 10–11), apparently expanding in size away from theca for some distance before becoming smaller again; in theca about 15 mm long, brachioles from middle of am-



Text-Figure 20. Growth plots for six measured specimens (MCZ 871–876) of *Strongyloblastus laudoni*, n. sp. Because many specimens were incomplete, only 3–4 specimens could be plotted in some cases; short lines through some measurements indicate estimated values in broken specimens. Best-fit lines in all plots were hand fit.

bulacrum biserially-plated, about 18–19 mm long, 0.25 mm wide, and 0.3 mm deep, apparently a single set of distally slightly-imbricate brachiolar cover plates present, about 3.3 cover plates per brachiolar plate on each side, cover plates slightly arched over brachiolar food groove (Text-Fig. 18I). In holotype, tiny cover plates scattered over ambulacra and still organized into domed structure over adoral food grooves and central mouth (Plate 6, Figs. 28–29); many basal brachiolar plates still attached to edges of ambulacra in this specimen. Stem preserved in three paratypes; in theca about 15 mm long, 4.5 mm of proximal stem preserved, decreasing from 1.5 mm at theca to 0.8 mm at preserved distal tip, proximal columnals thin, expanding to basal attachment, about 5 per mm, distal columnals thicker, about 3 per mm (Text-Fig. 18G).

Studied Specimens. Holotype MCZ 871, paratypes MCZ 872–881 (10 specimens and plates), and MORI 001 (Welch Collection, Museum of the Rockies, Montana State University, Bozeman); 11 additional plates in MCZ 883.

Occurrence. Known from two localities in the Bridger Range, southwestern Montana, and one locality in the Little Belt Mountains, west-central Montana: all except one MCZ specimen from Northeast Baldy Mountain in the southern Bridger Range (21 specimens and plates, including the holotype) from two 6–8 in. (0.15–0.20 m) beds in the middle Paine Member about 150–175 ft (46–53 m) above the base of this member, single ambulacrum from the float about 115 ft (35 m) above the base at Baldy Mountain just to the south, and a single complete specimen from an unknown Lodgepole horizon at Ant Park in the Little Belt Mountains (Welch Collection).

Etymology. Named for Lowell R. Laudon, formerly at the University of Wisconsin, Madison, who first discovered complete blastoids in the Bridger Range and directed us to the rich Northeast Baldy Mountain locality in 1966.

Discussion. Strongyloblastus laudoni retains its juvenile obconical shape with a shorter vault and ambulacra and a lower pelvic angle into the adult stage instead of becoming elongate ellipsoidal as *S. breimeri* does. Other minor differences include the hypodeltoid apparently not being enlarged in *S. laudoni,* and the lancet occupying somewhat less of the ambulacral width; however, other features of the ambulacra, pore development, half-paired anispiracle, and anal deltoids are very similar. This species is also similar to *S. kirki* (see *Strongyloblastus* Discussion) but is less elongate with a lower L/W ratio and a higher pelvic angle, has a smaller stem facet, no pores along most of the deltoid because the deltoid edge is ridged, and may show other differences in the anispiracle and anal deltoids.

STRONGYLOBLASTUS SP.

Plate 6, Figs. 21–23;
Text-Figures 18J–K and 19

A single small specimen from the lower Lodgepole Limestone apparently does not belong to either of the named species of *Strongyloblastus* known from this formation. This specimen (MCZ 870) is immature (5.5 mm long), but is well preserved and not like similar-sized specimens of *S. breimeri* or *S. laudoni* in its shape. It is briefly described here but not named.

Description. Specimen godoniform in shape (Text-Fig. 18J), relatively wide, interambulacra flat to slightly concave; theca 5.5 mm long, 5.2 mm wide, L/W ratio = 1.1; vault widely parabolic, slightly recurved, 3.5 mm long, pelvis low conical, slightly concave in profile, 2.0 mm long, V/P ratio = 1.8; pelvic angle 100–105°, much higher than either of the other Lodgepole species at this size. Basals three, relatively large, make up 50–60% of pelvis, slightly bulbous with small stem facet; radials five, large, fairly long, raised above ambulacra; regular deltoids four, very short, but just appearing on side of theca; ambulacra moderately long but without many side plate sets, slightly convex, am-

bulacral pores appear to die out just above radiodeltoid suture; spiracles well divided by deltoid septa, "C" spiracle separated from rest of half-paired anispiracle (Text-Fig. 18K); ornament consists of relatively coarse growth lines with several of these raised (Plate 6, Fig. 21).

Growth features included with *S. breimeri* for comparison (Text-Fig. 19).

Studied Specimen. MCZ 870.

Occurrence. Known from the lower Paine Member, Lodgepole Limestone, from beds 22–33 ft (7–10 m) above the base at Targhee Peak, just inside southeastern Idaho.

Discussion. This specimen occurs with *Tanaoblastus* in the same beds of the lower Lodgepole Limestone as *S. breimeri* normally does, but unless it is an abnormal growth variant, it does not appear to belong to this species. It also occurs in a different part of the field area from the narrow east-west strip where most specimens of *S. breimeri* have been found. This specimen is much wider with a lower L/W ratio and a larger pelvic angle than small specimens of *S. breimeri* (or *S. laudoni*); the raised growth lines are also different than most specimens of these species. Perhaps larger specimens of this form would also have been godoniform in thecal shape, but additional specimens will be necessary to determine this.

Family GRANATOCRINIDAE Fay, 1961
Subfamily CRYPTOBLASTINAE Fay, 1964
Genus TANAOBLASTUS Fay, 1961

Type Species. Pentremites roemeri Shumard, 1855.

Diagnosis. Spiraculate blastoids with a globular theca, ambulacra extending to base or nearly so, base moderately convex to flat, interradial sutures not depressed; eight widely separated spiracles and an anispiracle, two hydrospire folds beneath each side of ambulacrum; four anal deltoids, adoral superdeltoid, aboral hypodeltoid, and two hidden cryptodeltoids lying beneath hypodeltoid; regular deltoids of moderate size usually visible in side view, occupying from one-sixth to nearly one-half of thecal length, hypodeltoid usually slightly enlarged over regular deltoids, radials usually overlapping deltoids; ambulacra long and relatively narrow, lancet partly exposed toward adoral end, hydrospire plate present along radials bearing between 1.0 to 1.6 pores per side plate, pores usually absent along deltoids except for 1–3 pores located just above radiodeltoid suture in several species.

Occurrence. Early Mississippian (Late Kinderhookian = Late? Tournaisian), central and western U.S.A. (Missouri, Montana, Idaho, Utah, Wyoming?, Nevada?, Arizona?).

Discussion. Tanaoblastus differs from other closely related genera, such as *Cryptoblastus*, by having a slightly different thecal shape without depressed interradial sutures and by having a flat to moderately convex base. It differs from *Mesoblastus* by having only two hydrospire folds per side, a different number of pores along the radials, and larger but less ornamented deltoids. Two species of *Tanaoblastus* are especially abundant in western Montana and adjacent areas such as southeastern Idaho and northernmost Utah. Very similar species apparently occur in the early Mississippian of Missouri, especially in the Chouteau Limestone. None of the Montana material shows the hidden cryptodeltoids on the anal side, and it is still uncertain whether *Tanaoblastus* has four anal deltoids as Fay (1961) reported or whether it might be more advanced and have only two anal deltoids, an epideltoid, and a hypodeltoid. The Montana material studied here probably makes up the largest collections of *Tanaoblastus* that have ever been assembled.

TANAOBLASTUS HAYNESI (Clark), 1917

Plate 1, Figure 1; Plate 7, Figures 1–30; Text-Figures 21A–B, E–F, H, and 22

Schizoblastus haynesi, Clark, 1917, pp. 371–373, plate 1, figures 15–20.

Mesoblastus haynesi, Fritz and Cline, 1937, pp. 308–

309, plate 17, figures 10–12 (but not plate 17, figures 1–9).
Tanaoblastus haynesi, Fay, 1961, pp. 102 and 104, plate 37, figures 7–9.

Diagnosis. Theca globular, L/W ratio varies from about 0.9–1.2; ambulacra almost reaching base in small individuals, reaching base and protruding slightly in large ones; basals flat to moderately convex, fairly small, deltoids occupying one-third of theca length in small individuals, about one-sixth of thecal length in large ones, interambulacra flat to slightly concave; spiracles wide apart on summit, last pore at radiodeltoid suture; ornament consists of fine growth lines on radials, coarser bands along RD fronts, low ridges on basals.

Description. About 925 specimens of this species available for study from about 30 localities in western Montana (Table 1), ranging throughout the lower 75 ft (23 m) of the Lodgepole Limestone. The following description is based on the holotype specimen MCZ 347 described by Clark (1917) and about 40 other newly-collected specimens.

Theca globular, varying from elongate to squat, small thecae nearly spherical, larger ones more variable; vault rounded, pelvis slightly convex, basals moderately convex to flat, interambulacra usually slightly concave, but may be flat in some specimens, greatest width near midheight; smallest theca about 2.8 mm long, largest theca about 10 mm long and 9 mm wide (Plate 7, Figs. 1–25).

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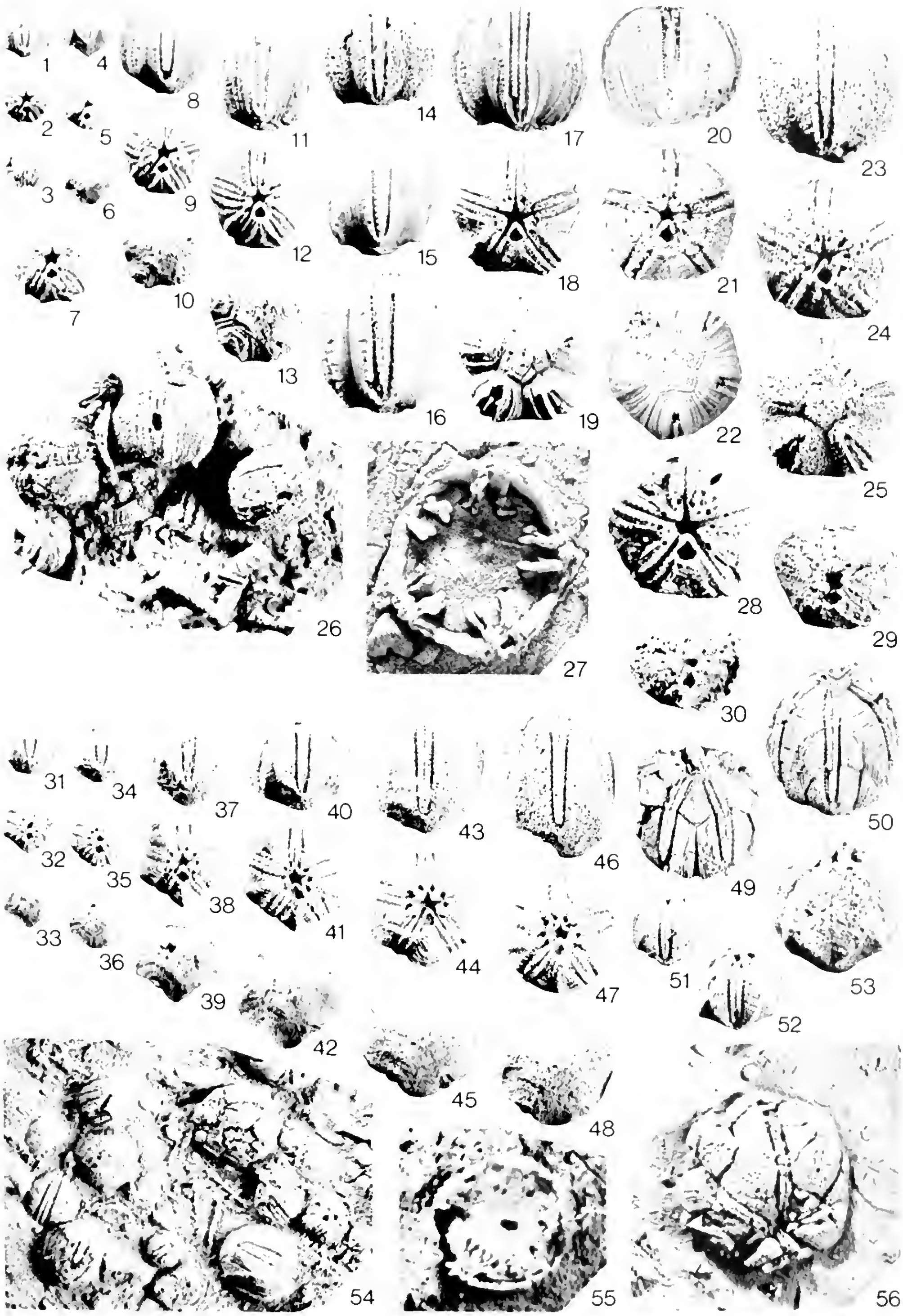
PLATE 7

Figures 1–30. *Tanaoblastus haynesi* (Clark), lower Paine Member, lower Lodgepole Limestone, 1–3 from Brazer Canyon, northeastern Utah, 4–6 and 8–13 from Targhee Peak, southeastern Idaho, 7 from White Peak, 14 and 17–19 from Squaw Creek, 15 from North Sawtooth Mountain, northwestern Montana, 16 from Northeast Baldy Mountain, 20–22 from Old Baldy Mountain, 23–25 and 29–30 from London Hills, 26 from Cowboy Canyon, 27 from Timber Butte, and 28 from Sixteen Mile Creek, all except 1–6, 8–13, and 15 from southwestern Montana. 1–3, D-side, top, and bottom views of very small theca USNM 16515 showing raised radial edges alongside ambulacra, ×2.7; 4–6, E-side, top, and bottom views of very small theca MCZ 1030; note relatively short ambulacra and nearly round cross section, ×2.7; 7, top view of medium-sized theca USNM 20163 showing eight spiracles and anispiracle, ×2.7; 8–10, B-side, top, and bottom views of medium-sized theca MCZ 1027; note globular shape and pentagonal cross section, ×2.7; 11–13, C-side, top, and bottom views of medium-sized elongate theca MCZ 1031 showing ornament, enlarged and slightly raised hypodeltoid, and partly-exposed lancet, ×2.7; 14, B-side view of medium-sized squat theca USNM 20602 having rather coarse silicification, ×2.7; 15, C-side view of large elongate theca MCZ 1026; note fine ornament and flat interambulacra, ×2.7; 16, C-side view of medium-sized elongate theca MCZ 1067 showing plate ornament, ambulacral pores ending at radiodeltoid suture, and slight lancet exposure, ×4; 17–19, A-side, top, and bottom views of large squat theca USNM 20603; note fine ornament, raised basals, and slightly concave interambulacra, ×2.7; 20–22, E-side, top, and bottom views of large squat holotype MCZ 347 showing ornament, short but visible deltoids, and relatively large flat basals (A ray at bottom), ×3.0; 23–25, D-side, top, and bottom views of very large elongate theca MCZ 1028; note coarse silicification, small raised basals, and missing side plates, ×2.7; 26, cluster of seven small to medium-sized thecae on partly-etched slab MCZ 1038, ×3.2; 27, cross section MCZ 1025 showing two well-preserved silicified hydrospires beneath each ambulacral edge, ×5; 28, enlarged top view of theca MCZ 1035; note eight spiracles and anispiracle plus well-preserved ambulacra, ×4; 29–30, top views of abnormal thecae MCZ 1036 and 1037, both of which lack the A ambulacrum, ×3.2.

Figures 31–56. *Tanaoblastus allanensis* Sprinkle and Gutschick, n. sp., lower Allan Mountain Limestone, four localities around Crown Mountain, northwestern Montana. 31–33, E-side, top, and bottom views of small angular paratype MCZ 964 showing ambulacra not reaching base of theca, ×2.8; 34–36, C-side, top, and bottom views of small rounded paratype MCZ 965; note well-preserved spiracles and anispiracle, ×2.8; 37–39, C-side, top, and bottom views of medium-sized very angular paratype MCZ 968 showing pentagonal cross section and depressed ambulacra, ×2.8; 40–42, A-side, top, and bottom views of medium-sized angular paratype MCZ 970; note long deltoids and abnormal basals (three azygous, one zygous), ×2.8; 43–45, B-side, top, and bottom views of large rounded holotype MCZ 963 showing ornament on large deltoids and convex base with secondary deposits around small stem facet, ×2.8; 46–48, C-side, top, and bottom views of large rounded paratype MCZ 972; note large deltoids with low central ridge and rounded cross section, ×2.8; 49, AB? interray view of large crushed paratype MCZ 975 showing plate sutures and ornament, ×2.7; 50, B-side view of large crushed paratype MCZ 977; note well-preserved ornament and few ambulacral pores above radiodeltoid suture, ×2.7; 51, oblique E-side view of rounded paratype MCZ 967 showing few pores alongside lower deltoids, ×2.7; 52, oblique E-side view of angular paratype MCZ 976; note ambulacrum, spiracles, and few ambulacral pores above radiodeltoid suture, ×2.7; 53, oblique E-side view of abnormal paratype MCZ 969; E ambulacrum and its lancet missing and surrounding thecal plates in contact across sinus, ×4; 54, cluster of nine or more small to medium-sized thecae on paratype slab MCZ 978, ×2.5; 55, paratype cross section MCZ 974 showing holes for hydrospires in chert-filled interior, ×4.3; 56, oblique top view of very large crushed paratype MCZ 973 in slab; note large deltoids and broken thecal plates, ×2.5.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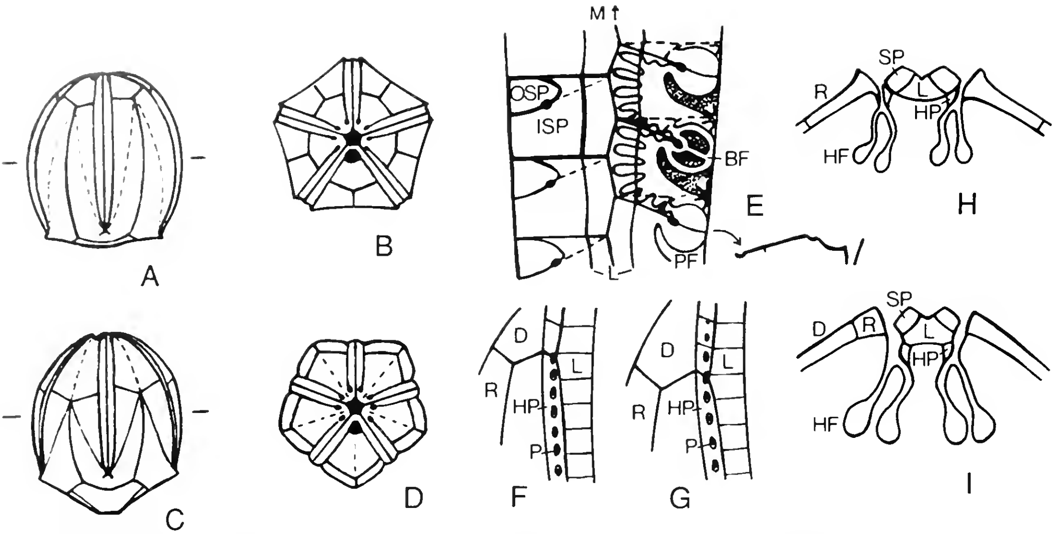


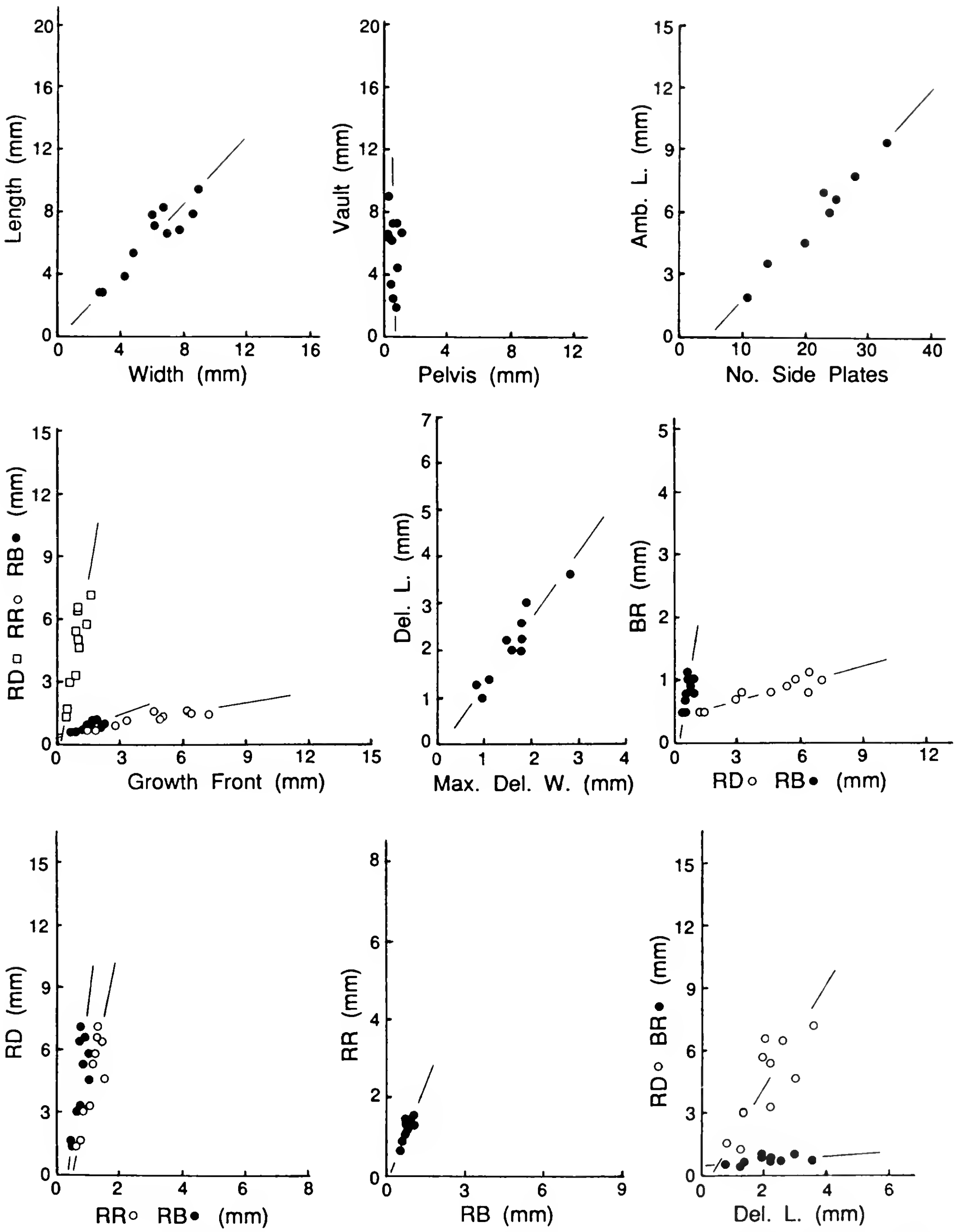
Text-Figure 21. Morphologic features of *Tanaoblastus haynesi* (Clark) (A–B, E–F, H) and *T. allanensis*, n. sp. (C–D, G, I). A–D, side and summit views of large elongate thecae showing maximum width (short lines) near midheight, longer deltoids and shorter ambulacra in *T. allanensis* (C–D), and difference in interambulacral shape (flat to slightly concave in *T. haynesi* vs. convex to humped in *T. allanensis*). E, enlarged ambulacrum in figured *T. haynesi* specimen MCZ 1024; note central lancet (L) and inner and outer side plates (ISP and OSP) supporting large brachiole facets (BF) at edge of ambulacrum with pore furrow (PF) wrapping around lower edge; cross section is along side food groove and facet, and small arrow points toward mouth (M). F–G, comparison between *T. haynesi* (F) and *T. allanensis* (G) showing that pores (P) through hydrospire plate (HP) either stop at suture between radials (R) and deltoid (D) when side plates missing from lancet (L), or extend short distance further along deltoid edge; F drawn from specimen MCZ 1024, G from paratypes MCZ 965 and 967. H–I, cross sections of ambulacra in *T. haynesi* specimen MCZ 1025 (H) and *T. allanensis* paratype MCZ 974 (I); note lancet (L) overlapped by side plates (SP) in ambulacra and shape of two hydrospire folds (HF) and hydrospire plate (HP) beneath each side of ambulacrum and adjacent radial (R) or deltoid (D).

Basals three, normally arranged, two larger and one smaller (azygous), usually slightly convex in profile except in small thecae where moderately convex, relatively small, occupying 50 to 60% of pelvis (Plate 7, Figs. 19, 22, and 25). In medium-sized theca, azygous basal 1.6 mm long, 1.6 mm wide, larger basals about same length, and 2.4 mm wide. Center of basal set covered with thin secondary deposits obscuring growth lines and bearing central stem facet about 0.7–0.9 mm in diameter, with about 25–26 crenulae extending one-fourth of distance in from margin, and small round central lumen about 0.07–0.08 mm in size surrounded by a slightly depressed region (Plate 7, Fig. 19).

Radials five, large, making up most of thecal surface (greater than 60%), recurved at base with short body occupying 40–50% of pelvis, and long moderately curved limbs enclosing long ambulacral sinus. Radiodeltoid suture nearly straight, RD axis dominates growth (Text-Fig. 22), small radial lip near origin of radials pointing outward or slightly downward.

Regular deltoids four, relatively small, make up 16–20% of length in large thecae, DR suture makes angle of about 135°; deltoid lips small, form edges of mouth, two elliptical spiracles notched in aboral corners of lip with small ridge around inside edge of spiracles; deltoid body larger, diamond-shaped, moderately concave adorally, slightly concave to flat aborally, radials slightly overlap deltoids at radiodeltoid suture.

Anal deltoids apparently four, adoral superdeltoid (=lip of regular deltoids), two deep, hidden cryptodeltoids (forming septa separating anus from posterior hydrospires beneath hypodeltoid), and large aboral hypodeltoid (=regular deltoid bodies), hypodeltoid slightly enlarged over other del-



Text-Figure 22. Growth plots for 11 measured specimens (MCZ 1026–1028, 1030–1031, 1066–1067, holotype MCZ 347, USGS 16815 and 20602–20603) of *Tanaoblastus haynesi* (Clark). Note that the pelvis shows no apparent growth in its contribution to thecal length (top center) and very slow growth in RB and RR. Best-fit lines in all plots were hand fit.

toid bodies. Anispiracle nearly circular, formed by superdeltoid adorally, hypodeltoid aborally, and small segment of side plates from adjacent adoral ambulacra laterally (Plate 7, Figs. 18 and 21).

Mouth central on summit, formed by regular deltoid lips plus superdeltoid, pentagonal to slightly star-shaped, slightly larger than anispiracle, has lobes and sockets on margins.

Ambulacra five, long and fairly narrow, usually extending to or near base, moderately curved along length, moderately to strongly convex (actually biconvex) in cross section (Text-Fig. 21E), highest points at or slightly above level of adjacent thecal plates, edges slightly depressed below thecal plates, widest at radiodeltoid suture, lancet slightly exposed along most of length, about one-third to one-half of its width exposed, occupying about one-fourth to one-third of ambulacral width, side plate sets on bevelled lancet edge, inner side plates modified rectangular, outer side plates small and triangular, occupy abmedial aboral margin of inner side plates, each set of inner and outer side plates bears a fairly large, nearly circular, brachiole facet at edge of ambulacrum, small round brachiolar pit near highest point of ambulacrum at end of side food groove, two depressed facets just abmedial to this, where brachiolar plates attached (Text-Fig. 21E). Large pore furrow curving around aboral side of brachiole facet; 3–4 lobes along main food groove usually in lancet material, 3–4 lobes adorally and usually two lobes aborally along short side food grooves mostly on inner side plates. Hydrospire plate present along radials beneath edge of ambulacra, formed by radial material, side plate impressions on lancet and adjacent deltoid edge but not on adjacent radial edge or hydrospire plate (Text-Fig. 21F), one row of pores in hydrospire plate, between 1.5–1.6 pores per side plate set, pores slightly elongate along ambulacral length, last pore at radiodeltoid suture round to very elongate, apparently place where new pores inserted.

Hydrospires in 10 groups, two folds per ambulacral side, folds hang down into thecal cavity (Text-Fig. 21H; Plate 7, Fig. 27), folds have thin parallel walls and an enlarged tube at bottom.

Ornament consists of fine growth lines along RR front with slightly pustular periodic markings, basals have closely spaced pustular periodic markings, relatively coarse growth lines on RD fronts expanding towards deltoids, DR growth front variable ranging from fine growth lines to fairly coarse pustule-bearing bands (Plate 1, Fig. 1). Radials and deltoids have raised nodes along ambulacra, moderate secondary deposits forming stem facet, slight secondary deposits forming radial lips, edges of ambulacra, and slightly raised adoral edge of hypodeltoid.

Measurements of growth series specimens plotted in Text-Figure 22. Small specimens have a fairly large convex base with short ambulacra, a relatively small V/P ratio, and fairly large deltoids. Large specimens tend to become more elongate or more squat with relatively small base, ambulacra usually reaching base, higher V/P ratio, and deltoids occupying less of thecal length.

No stems or brachioles known for this species. Three abnormal specimens in about 925 examined (0.3%), all of these four-sided with an ambulacrum that remained very small or never developed. Radials and deltoids appear normal, but radial sinus closed and deltoids in lateral contact; two abnormalities affect "A" ambulacrum, one affects "D" ambulacrum, very small spiracles possibly present in abnormal ray (see Plate 7, Figs. 29–30).

Studied Specimens. Holotype MCZ 347, paratypes MCZ 341; other studied or measured specimens MCZ 1024–1038, USGS Collections 16815, 20163, and 20602–3; other specimens MCZ 1039.

Occurrence. Known from between 5 and 75 ft (1.5–23 m) above the base of the Paine Member of the Lodgepole Limestone at 30 or more localities in southwestern and west-central Montana, south-

eastern Idaho, and northeastern Utah; also found in the lower Allan Mountain Limestone at North Sawtooth Mountain in northwestern Montana (see Table 1).

Discussion. Tanaoblastus haynesi characterizes the lower Paine Member of the Lodgepole Limestone in much of western Montana, southeastern Idaho, and northeastern Utah. This blastoid seems to be present at most sections of the Montana Facies of Sando (1976). The preservation of these silicified specimens ranges from only fair (see Plate 7, Figs. 23–25), at localities such as London Hills, to excellent when extracted with acetic acid at localities such as Standard Creek (see Plate 1, Fig. 1) and Targhee Peak (Plate 7, Figs. 8–13). This species is similar to several species from the Mississippi Valley, such as *T. missouriensis* and *T. tenuis*; it differs from these species by usually being less elongate, by having flat to slightly concave interambulacra, by having somewhat stronger growth bands on the basals and periodically on the radials, by having a somewhat different number of pores per side plate set along the radials, and by having different length (usually shorter) deltoids. *Tanaoblastus haynesi* differs from *T. allanensis*, n. sp., by having a shorter base, flat to slightly concave interambulacra, the last pore at the radiodeltoid suture, and shorter deltoids.

TANAOBLASTUS ALLANENSIS
Sprinkle and Gutschick, new species
Plate 7, Figures 31–56;
Text-Figures 21C–D, G, I, and 23

Diagnosis. Theca globular, length nearly equal to width, V/P ratio averaging 3.1, interambulacra moderately convex to strongly angular; deltoids long, occupying between one-third and one-half of thecal length, radials abut deltoids; ambulacra relatively long, not reaching base of theca, 1–3 pores just above radiodeltoid suture; ornamented with moderately coarse growth lines.

Description. At least 174 specimens available for study, all from four localities in the lower Allan Mountain Limestone at Crown Mountain in northwestern Montana. Holotype MCZ 963, and 16 other paratypes used for the following description.

Theca globular to elongate, sometimes squat, rounded to flaring pentagonal in cross section, vault rounded, pelvis slightly to moderately convex, maximum width at or considerably above midheight, ambulacra flush with adjacent thecal plates; smallest theca 2.9 mm long, largest free theca about 8.3 mm long and 6.8 mm wide, very large obliquely crushed theca in slab at least 8.5 mm long and 11.5 mm wide; L/W ratio ranging from 0.85 to 1.21, averaging 1.0, V/P ratio ranging from 1.95 to 4.38, and averaging 3.1, pelvic angle ranging from 90° to 120° and averaging 112°, based on 10 specimens in growth series.

Basals three, normally arranged, two larger and one smaller (azygous), fairly small, make up 50–60% of pelvis, usually convex in side view with small stem facet (Plate 7, Fig. 42), in large specimen azygous basal 2.1 mm long and wide, larger basals about same length and about 2.8 mm wide.

Radials five, fairly large, make up much of thecal surface (about 50%), have small lip at radial origin, body fairly short, making up about 40% of pelvis, limbs fairly long, making up half or more of ambulacral sinuses, adoral end of radials raised, producing convex to angular cross section.

Regular deltoids four, fairly large, occupying one-third or more of curved ambulacral sinuses, between one-third and one-half of thecal length (Text-Fig. 21C), rhombic-shaped, aboral end strongly convex or crested to meet raised adoral radials, radiodeltoid suture forms angle between 90° and 130°, radials appear to abut deltoids without any overlap. Spiracles eight, slightly elliptical, at lateral margins of deltoid lips, about 0.6 mm apart across deltoids and across ambulacra, slight ridges just inside spiracles on edges of deltoids; mouth central on summit, about 0.6–0.7

mm in diameter, slightly wider than long, star-shaped to pentagonal, margins formed by regular deltoid and superdeltoid lips.

Anal deltoids apparently four, small superdeltoid adorally (=lips of other deltoids), two cryptodeltoids apparently hidden below hypodeltoid, and aboral, fairly large hypodeltoid (=body of other deltoids); hypodeltoid either same size or slightly enlarged over other deltoids, raised and slightly hooded adorally over anispiracle, which is surrounded by superdeltoid adorally, few side plates of ambulacra laterally, and hooded hypodeltoid aborally, anispiracle rounded to pentagonal, slightly smaller than mouth, about 0.6 mm in diameter. Cryptodeltoids difficult to see, may form septa separating posterior hydrospires from anus deep within anispiracle.

Ambulacra five, relatively long but not reaching base of theca, rather narrow, flush with or slightly depressed below adjacent thecal plates, slightly to moderately convex; lancet slightly exposed along most of length, occupying one-fourth to one-third of ambulacral width, mostly forming main food groove and adjacent lobes in center of ambulacrum, side food grooves enter main food groove at 40–70° angle. Side plates normally developed, inner side plates rectangular, small triangular outer side plates notch aboral abmedial edge of inner ones, together supporting relatively small brachiole facet at edge of ambulacrum. Between side food grooves, 4–5 lobes along main food groove, usually 3 adoral lobes and 2 small aboral lobes along each side food groove, which leads to small brachiolar pit and two small hemispherical depressions where brachiole attached. Pores developed in hydrospire plate alongside ambulacra, side plates do not completely cover hydrospire plate and pores, average of about 1.2 pores per side plate set along radials, pores absent along much of deltoid except at aboral end where 1–3 extra pores located just above radiodeltoid suture (Text-Fig. 21G).

Hydrospires in 10 groups, two hydrospires per ambulacral side, folds hang down into thecal cavity with thin lamellae and enlarged tubes at bottom, entrance to hydrospires through pores in hydrospire plate (Text-Fig. 21H; Plate 7, Fig. 55).

Ornament consists of moderate to fairly coarse growth lines on basals, radials, deltoids, and hypodeltoid, ornament along RD and DR fronts especially coarse (Plate 7, Figs. 44 and 50). Secondary deposits minor, forming stem facet and small radial lips.

Measurements of 10 specimens in growth series plotted in Text-Figure 23. Relatively little change in thecal shape with increasing size.

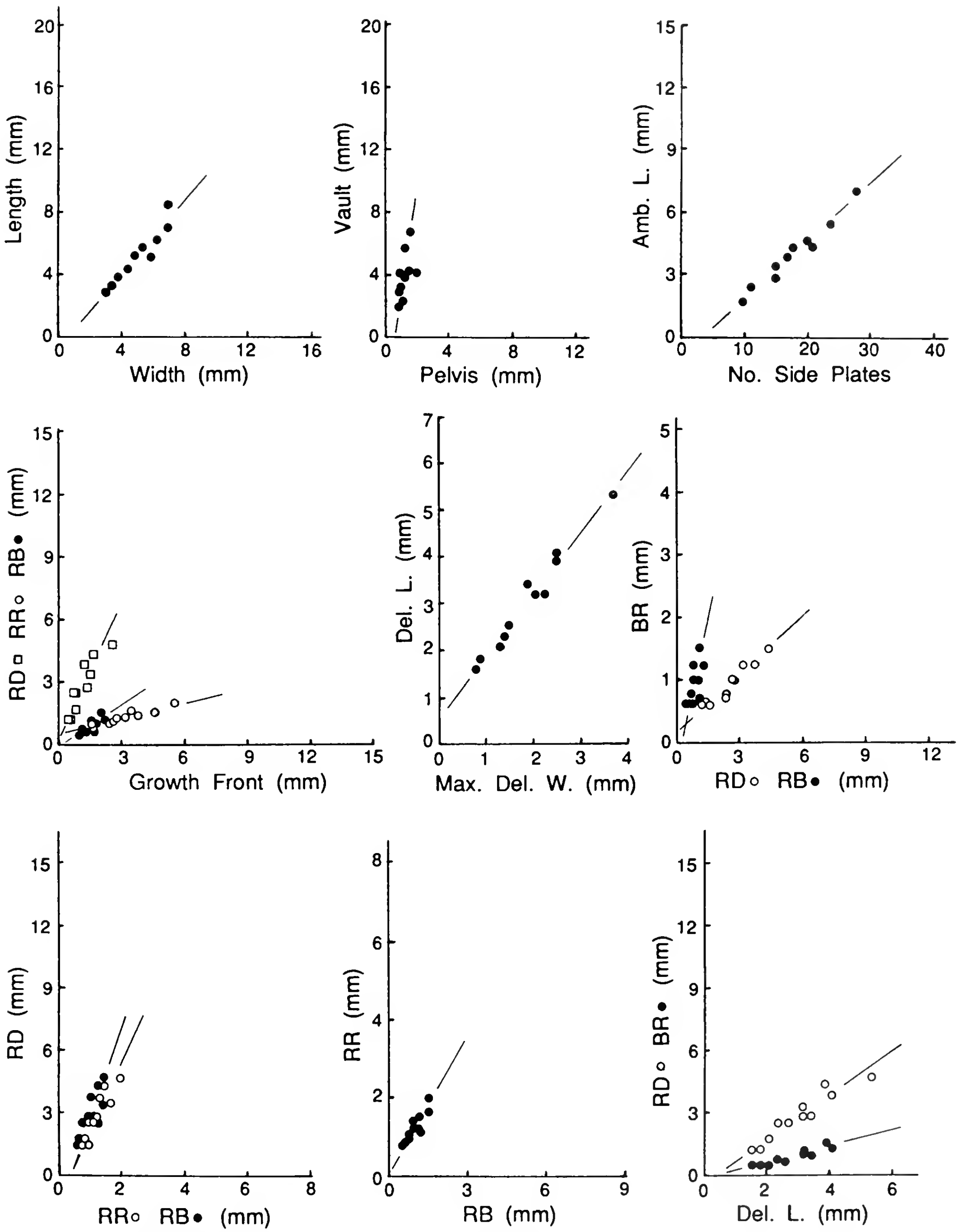
No stems or brachioles known for this species. Two abnormal thecae found in 174 examined (1.1%); one has no "E" ambulacrum although "E" radial appears normal-sized with limbs in contact and DE and EA deltoids abut each other apparently with two tiny spiracles near normal positions (Plate 7, Fig. 53). Other theca has four basals, one larger and three smaller; one of larger basals (apparently DA) split into two smaller plates, resembling azygous AB basal.

Studied Specimens. Holotype MCZ 963, paratypes MCZ 964–979, other additional specimens MCZ 980.

Occurrence. All studied specimens come from the area around Crown Mountain, between 11 and 35 ft (3.5–11 m) above the base of the Allan Mountain Limestone in northwestern Montana.

Etymology. Named for the Allan Mountain Limestone, where this species occurs.

Discussion. Tanaoblastus allanensis appears to be a paedomorphic derivative of some other *Tanaoblastus* species, perhaps *T. haynesi* which also occurs in the Early Mississippian of western Montana. It shows considerable resemblance to the juvenile specimens of this species and some similarity to species known from the Chouteau Limestone in Missouri. The convex base, long deltoids, relatively long ambulacra that do not reach the base, and convex to angular shape in cross section are all features similar to juveniles of *T. haynesi*,



Text-Figure 23. Growth plots for 10 measured specimens (MCZ 863–872) of *Tanaoblastus allanensis*, n. sp. Note slow growth in pelvis because of slow growth in RB and BR. Best-fit lines in all plots were hand fit.

although the cross section is not so angular in that form. The small size of most adult specimens of *T. allanensis* may also agree with this possible derivation. *Tanaoblastus allanensis* shows some resemblance to Mississippi Valley forms such as *T. tenuis* (Hambach) and *T. roemeri* (Shumard) in its globular cross section and protruding base, but the deltoids are not so angular in either of these Missouri forms and the base is much less pronounced than in *T. allanensis*. These Chouteau species do not differ much among themselves, and we question whether all of these are really distinct species.

The cross-sectional profile of *T. allanensis* is probably the most variable feature of this species. Rounded forms and highly angular forms are fairly easy end members to pick out of the available material, but many intermediates exist and some forms cannot be assigned to one or the other with any certainty. We considered the possibility that two separate species might be present in this Crown Mountain material, but decided that these are probably highly variable individuals in a single species because of the many intermediates and the occurrence of both forms at all four of the Crown Mountain sections. The angularity in cross section probably represents a growth feature that was not highly controlled genetically.

Genus CRYPTOBLASTUS Etheridge and Carpenter, 1886

Type species. Pentremites melo Owen and Shumard, 1850.

Diagnosis. Spiraculate blastoids with an ellipsoidal or ovoid theca, base fairly small, usually with small, depressed basals; eight spiracles plus an anispiracle; four anal deltoids present, small adoral superdeltoid, two deep, hidden cryptodeltoids, and aboral hypodeltoid that is not enlarged; ambulacra long, slightly depressed, extend to base of theca, lancet slightly exposed along most of length, hydrospire plate present with about 1.5 pores per side plate set along radials, pores absent along deltoids; interradial sutures often depressed, radials overlap deltoids.

Occurrence. Early to Middle Mississippian (Kinderhookian to Osagean), Mississippi Valley and northwestern Rockies, plus southern Canadian Rockies.

Discussion. At least five species of globular blastoids occur in the U.S. and Canadian Rockies that may belong to *Cryptoblastus*; three of these occur in the Lodgepole Limestone in western Montana. Two other species, including the form called *Mesoblastus haynesi* described by Fritz and Cline (1937) and a form that occurs in the Banff Formation near Lake Minnewanka in southern Alberta, also appear to belong to *Cryptoblastus*. The three Lodgepole species occur in the middle and upper parts of this unit at different localities; unfortunately, none of them is particularly common, complete, or well preserved. For this reason they are not formally named in this paper, but are only briefly described and illustrated.

CRYPTOBLASTUS? species A
Plate 4, Figures 14–28;
Text-Figures 24A–D and 25

About 11–12 silicified specimens and several fragments and plates from two localities near the top of the Lodgepole Limestone appear to belong to one species of *Cryptoblastus*. This species has an ellipsoidal theca with a rounded vault and a medium-sized base having a concave basal cavity, a L/W ratio ranging from 1.04 to 1.32, averaging 1.15 in the five nearly complete specimens, relatively short deltoids, and nearly paired, closely set spiracles.

Theca ellipsoidal, base medium-sized, depressed in center, profile in oral view pentagonal with flat to slightly convex interambulacra. Large, nearly complete theca 8.0 mm long, 7.6 mm wide, vault occupying entire length, pelvis depressed, basals inset about 1.0 mm above tips of ambulacra. Basals three, small, make up shallow basal cavity, deepest part occupied by fairly small stem facet about 1.0 mm

in diameter; radials five, very large, occupy about 80% of thecal surface, strongly recurved at base with short body about 1.5 mm long and long limbs about 7.0 mm long; deltoids four, short, barely appearing on side of theca, body about 1.2 mm long, with short lip adorally; hypodeltoid also small, not enlarged, apparent superdeltoid slightly wider than other deltoid lips, cryptodeltoids not seen but thin septa internally separate anus from posterior spiracles; eight closely spaced spiracles on summit, thin septum connects deltoid body and lip, and barely separates spiracles at surface, spiracles widely separated across adjacent ambulacra. Ambulacra five, long, extending to base of theca, where small radial lips present, ambulacra convex and angular, nearly flush with adjacent thecal plates, lancet appears slightly exposed along most of length, side plates numerous, hydrospire plate with 1.5–1.6 pores per side plate set along radials, pores apparently absent along short deltoids, thin raised ridges on edges of radials and deltoids. Ornament consists of fine growth lines with small pustules on radials, coarser growth lines on RD fronts and deltoids, radial body and basals nearly smooth.

Studied Specimens. MCZ 1045–1061 plus one theca and several plates in USGS Collection 20670 (Sando Collection).

Occurrence. Upper Lodgepole Limestone, most specimens from about 655 ft (200 m) above the base in the upper half of Woodhurst Member at Sacagawea Peak, northern Bridger Range, southwestern Montana; single specimen (MCZ 1059) with similar features in a float slab from an unknown footage in the upper Lodgepole? Limestone at Pole Canyon, northern Tobacco Root Mountains, southwestern Montana.

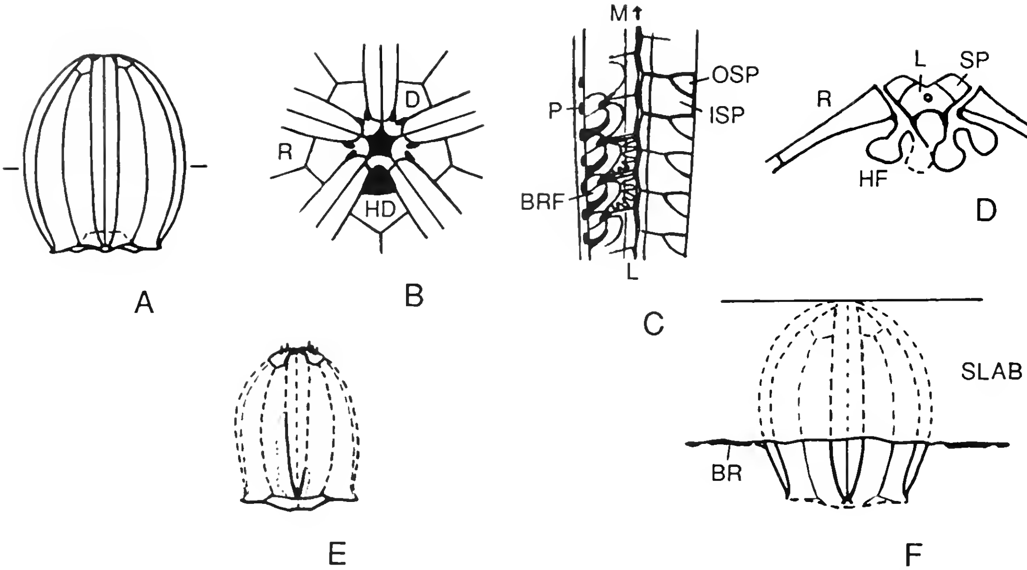
Discussion. This form has many features similar to *Cryptoblastus melo*, but some that are different. The medium-sized, slightly concave base is somewhat different, and this form lacks the depressed sutures that characterize *C. melo*. The number of anal deltoids is unknown; if it is four as suspected, this form would be most closely related to *Cryptoblastus* and has been questionably assigned to that genus here. More and better-preserved specimens will be necessary to confirm this assignment.

CRYPTOBLASTUS? species B
Plate 4, Figures 31–34; Text-Figure 24E

A small number of distinctive plates belonging to a globular blastoid were recovered from acid residues from the large *Koryschisma* block found at Bandbox Mountain in west-central Montana. This form is known from only four plates or fragments, but may also belong to *Cryptoblastus*. Available material includes a partial base with all three basals and parts of two radials, a partial radial with one nearly complete limb and ambulacral margin, and two small spine-bearing deltoids.

Base nearly flat, fairly wide, basals three, slightly convex, occupy 55–60% of short pelvis, stem facet protrudes slightly, about 1.2 mm in diameter, azygous basal about 1.9 mm long, 2.1 mm wide, larger basals about same length, about 2.5 mm wide, both basals and radial bodies ornamented with fine growth lines. Radial bodies short, limbs long, radials at least 6.5 mm long in largest fragment, ambulacra absent, but some evidence for pores along radial margin (in hydrospire plate?), radials have medium-sized lips pointing outward at tips of ambulacra, possibly two hydrospire folds per ambulacral side, ambulacra apparently narrow. Deltoids short, body ornamented with fairly coarse growth lines, adoral tip of deltoid body bears either two or three large spines (Plate 4, Fig. 31–32), thin septum leading from body to lip implies spiracles closely spaced or possibly paired, possibly two hydrospire folds beneath deltoid body leading to spiracles, radials appear to overlap deltoids, and radiodeltoid suture forms angle near 125°.

Studied Specimens and Occurrence. MCZ 1041–1044 from a block of limestone



Text-Figure 24. Morphology of *Cryptoblastus*? sp. A (A–D), *Cryptoblastus*? sp. B (E), and *Cryptoblastus*? sp. C (F). A, side view of large theca based on MCZ 1047 showing ellipsoidal shape (short lines at maximum width) with wide concave base, long fairly narrow ambulacra, and short deltoids just visible in side view, ×3.3. B, enlarged summit view in MCZ 1046; note closely set spiracles, small deltoids (D), and hypodeltoid (HD), ×5. C, plan view of ambulacrum based on MCZ 1050 and 1056 showing lancet (L) slightly exposed in center, large inner and small wedge-shaped outer side plates (ISP and OSP), and small brachiole facet (BRF) at edge of ambulacrum alongside hydrospire plate with pores (P), ×6.6. D, cross section of ambulacrum in MCZ 1054; note lancet (L) mostly covered by side plates (SP) and two hydrospire folds (HF) beneath each side of the ambulacrum, ×5. E, reconstructed thecal shape based on fragments MCZ 1041–1044 showing slightly convex base and spiny deltoids, ×2.5. F, reconstructed thecal shape in MCZ 1040 which is mostly buried in a slab and draped with brachioles (BR), ×3.3.

about 170–175 ft (52–53 m) above the base of the Paine Member, Lodgepole Limestone, at Bandbox Mountain, Little Belt Mountains, west-central Montana. This species is apparently a rare spiraculate occurring with the fissiculate *Koryschisma elegans*.

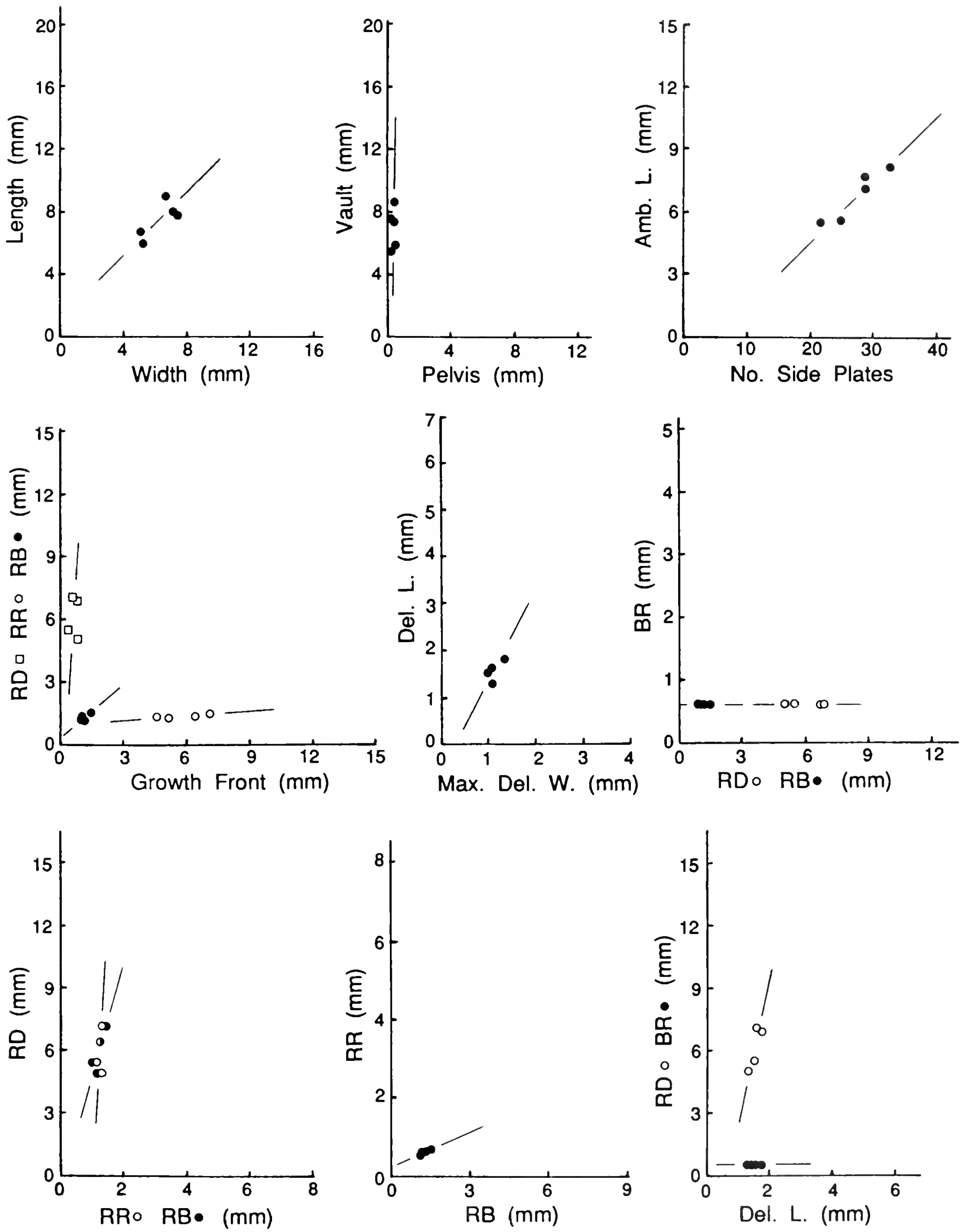
Discussion This species has a flat to slightly convex base and spiny deltoids unlike the other species of *Cryptoblastus*? and unlike the type species *C. melo*. The species is probably new but is not named here because of the fragmentary specimens.

CRYPTOBLASTUS? species C

Plate 4, Figures 29–30; Text-Figure 24F

This form is known from a single specimen from the middle Lodgepole Limestone at Northeast Baldy Mountain, southern Bridger Range, southwestern Montana. It occurs with numerous specimens of *Montanablastus baldyensis* and less common specimens of *Strongyloblastus laudoni*. The specimen is sitting vertically in a slab of limestone with the base exposed, weathered, and partly silicified; brachioles are splayed out on the slab surface from all five ambulacra (Plate 4, Figs. 29–30).

Ambulacra long and recurved, apparently reaching base of theca; using growth lines and internal calcite, base of theca (now eroded) apparently slightly convex and basals small to medium in size. Radials long with fine growth lines, ambulacra long, fairly narrow, with many side plate sets, brachioles still preserved attached to all five ambulacra, at least 18 mm long and about 0.2 mm wide, fairly well preserved, brachiolar plates 0.25 mm long and deep, food groove not seen except in cross sections where filled with pyrite specks. Back of slab ground down perpendicular to thecal axis to intersect summit (Text-



Text-Figure 25. Growth plots for five measured specimens (MCZ 1045–1047, 1049, and 1055) of *Cryptoblastus*? sp. A. Note that the pelvis hardly contributes to the length in side view (top center) and that BR shows no increase in size in these few specimens. Best-fit lines in all plots were hand fit.

Fig. 24F), deltoids apparently short, no evidence of deltoid spines, arrangement on summit apparently eight spiracles plus anispiracle. Number of hydrospires unknown. Specimen apparently about 8 mm long, based on distance from exposed base to start of summit in section, at least 7 mm wide.

Studied Specimen and Occurrence. MCZ 1040 from beds 150–175 ft (46–53 m) above the base of the Paine Member, Lodgepole Limestone, Northeast Baldy Mountain, southern Bridger Range, southwestern Montana.

Discussion. This specimen appears to be different from either of the other *Cryptoblastus*? species known from the middle or upper Lodgepole Limestone. It is similar to *Cryptoblastus*? sp. B in having a slightly convex base and occurring in the middle Lodgepole, but apparently does not have spiny deltoids. It differs from *Cryptoblastus*? sp. A from the upper Lodgepole in the shape of its base and in having larger basals. Better-preserved material will be necessary to completely identify this isolated specimen.

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The Neotropical and Mexican Species of the Orb-Weaver Genera Araneus, Dubiepeira, and Aculepeira (Araneae: Araneidae)

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THE NEOTROPICAL AND MEXICAN SPECIES OF THE ORB-WEAVER GENERA *ARANEUS, DUBIEPEIRA,* AND *ACULEPEIRA* (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Although *Araneus* species are mainly Holarctic, 113 species are found in Mexico and the Neotropics. Of these, 43 species (38%) were previously known. Twenty names are newly synonymized. The greatest diversity in morphology and number of species is found in Mexico and Central America. South American species of this genus are difficult to separate for several reasons: most species for which both males and females are known belong to the same species group, resulting in a fauna of closely-related, similar species. Furthermore, several species are unusually variable. An additional difficulty is that the species-characteristic embolus of the male palpus is often hidden in the contracted palpus.

The new genus *Dubiepeira*, with the type species *Metepeira dubitata* Soares and Camargo, contains five species found in the Amazon drainage, only two of which were previously known.

Of 13 species found in the area and placed in *Aculepeira*, six were previously known, seven are new. One of these is Holarctic, five are South American. Six species of which males are unknown, all coming from Hispaniola, Mexico, and Central America, may not belong to *Aculepeira*.

A list gives the generic placement of 186 names previously catalogued in the genus *Araneus*. Another list gives 72 names that cannot be recognized because types are immature or lost, and illustrations inadequate.

INTRODUCTION

In 1969, when I started revising Neotropical and Nearctic species of Araneidae, I made an extensive visit to the British Museum to acquaint myself with various genera of Araneidae and Tetragnathidae. There I made pencil drawings of genitalia and habitus of type species of the Pickard-Cambridge and Keyserling collections. I revised the Nearctic species first because data for them were much more complete than for the Neotropical species. In the course of my work, I illustrated the genitalia of type species of all genera, and of types of the Neotropical species of the genera I was revising, and thus gathered a large collection of notes and illustrations. (I have made copies of these illustrations available to colleagues who work with orb weavers.) I expected work on Neotropical araneids to proceed rapidly but due to the huge collections that have accumulated, especially in Brazil but also in the AMNH and MCZ, the research has been slowed.

The most important part of a revision is to examine, redescribe and illustrate the type specimens of previously named species, and compare them with specimens of the collections on hand. Many old type specimens had never been illustrated; often the species were distinguished by coloration. Even though old type specimens are usually those of the most common species, often their identity remains unknown. The scarcity of specimens caused early arachnologists to name males and females separately; often a species was named a second or third time for specimens collected in a different country. The least important part of a revision is the description of new species, as the new species are likely to be less common. In this revision, as in two previous ones, only about one-third of the species were previously known, two-thirds are new. There are 20 new syno-

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[faded]ms of the 41 previously known species names.

Later literature citations of the early described species are commonly misidentifications. Vials of specimens used in revisions often contain determination labels, most of which are wrong. While the determiner may have examined illustrations or even the type specimen of the original name, he may not have known which features made the species distinct. In specimens examined for this revision, *A. bogotensis* and *A. lathyrinus* usually had correct labels, but other species were also labeled *bogotensis* and *lathyrinus*. Such misidentifications and obsolete synonyms give rise to erroneous collecting localities in checklists and catalogs, and are difficult to expunge from the literature.

Despite recent revisions of species of Araneidae and our growing knowledge of araneid orb weavers, some authors, under pressure to publish, ignore all previous work. These authors make new genera, species, even families, with inadequate illustrations of genitalia, but giving elaborate "spine counts" without any evidence that such macrosetae can be used to separate species in this family, or that the author is aware of prior literature.

It is unfortunate that editors and reviewers of systematic papers do not ask authors to show knowledge of previous literature when publishing on new taxa. It is far easier to make new species, new genera, and new families than to acquaint oneself with prior literature, which often is difficult to obtain and in a foreign language.

Bonnet (1961) tells us that of 22,398 spiders listed, more than half (15,560) have not been cited again and presumably have not been found again. (Forty percent of species described between 1758 and 1799, 44% of species described between 1800 and 1849, 55% of species described between 1850 and 1899, and 87% of species described between 1900 and 1939, have not been found again.) Results of this revision show that species originally adequately described and illustrated, and whose types are in existence and can be examined, can be found again. In *Araneus*, only four recognizable species (*concoloratus, anguinifer, microsoma, rufipes*) described before 1940 have no additional specimens in collections. All come from well-collected Central America, and must be considered rare species from specialized habitats.

The orb-weaver family Araneidae, one of the largest families of spiders, contains about 45 valid, previously named genera in the Neotropics and at least 10 new genera for species represented in collections by both males and females. Some species, however, are known only from females, some from males, and a few from juveniles of doubtful generic affinity. Should they be placed with the genus containing most similar species but not necessarily sharing synapomorphic characters, or should they be kept separate until the missing gender is found?

Roewer (1942) lists a total of about 700 species of Araneidae from the Neotropics described before 1940. Brignoli (1983) lists about 250 more, described between 1940 and 1981, for a total of about 950 nominal species. It is difficult to keep an accurate accounting because many common species have been named several times and because there are many new species. But the 13 genera revised up to the present contain perhaps one-third of the Neotropical Araneidae species. Large genera still to be revised are *Mangora*, *Cyclosa*, and *Eustala*. The species of almost all other Neotropical spider families have not been revised.

There is no doubt that many araneid species are rare or live in habitats difficult to sample, such as the crowns of trees. Lethal insect dusts used to bring down arthropods from the tops of trees might just make orb weavers hold on to their threads for dear life.

MATERIALS AND ACKNOWLEDGMENTS

A revisionary study requires examination of many specimens and assembly of much far-flung information; it is possible only with the cooperation of many others.

The specimens used for this revision belong to or are deposited in the collections listed below. I would like to thank their curators for making the specimens available.

AMNH	American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin
BMNH	British Museum (Natural History), London, Great Britain; P. Hillyard, F. Wanless
CAS	California Academy of Sciences, San Francisco, United States; W. J. Pulawski, D. Ubick
CNC	Canadian National Collections, Ottawa, Canada; C. Dondale
CUC	Cornell University Collection, kept in the AMNH; N. Platnick
CV	C. Valderrama A.
DU	D. Ubick
FSCA	Florida State Collection of Arthropods, Gainesville, United States; G. B. Edwards
IBNP	Inventario Biológico Nacional, San Lorenzo, Paraguay; J. A. Kochalka
INPA	Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil; J. A. Raphael
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert
JAK	J. A. Kochalka
JMM	J. M. Maes, León, Nicaragua
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury
MCN	Museu de Ciências Naturais, Porto Alegre, Brazil; A. Lise, E. Buckup
MCZ	Museum of Comparative Zoology
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; L. Avilés
MEG	M. E. Galiano
MHNB	Museo de Historia Natural, Bogotá, Colombia
MHNC	Museu de História Natural, "Capão da Imbuia," Curitiba, Brazil; L. Bittencourt, S. de Fátima Caron
MHNM	Museo de Historia Natural de Montevideo, Uruguay; R. M. Capocasale
MHNMC	Museo de Historia Natural, Medellín, Colombia; M. A. Serna D.
MHNSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; D. Silva D.
MIUP	Museo de Invertebrados, Universidad de Panamá, Panama; D. Quintero A.
MLP	Museo de La Plata, Facultad de Ciencias Naturales, La Plata, Argentina; R. F. Arrozpide
MNHN	Muséum National d'Histoire Naturelle, Paris, France; J. Heurtault, J. Kovoor
MNRJ	Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa
MNSD	Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic; B. C. Reynoso S.
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil; P. Vanzolini, L. Neme, J. L. M. Leme
MZUF	Museo Zoologico, Università, Florence, Italy; S. Mascherini
MZUT	Museo ed Istituto di Zoologia "La Specola," Università di Torino, Italy; O. Elter
NHRM	Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt
NMB	Naturhistorisches Museum, Basel, Switzerland; E. Sutter
NMI	National Museum of Ireland, Dublin, Ireland; J. P. O'Connor, P. J. O'Sullivan

PAN	Polska Akademia Nauk, Warszawa, Poland; A. Riedel, W. Starega, J. Proszynski, A. Slojewska
REL	R. E. Leech
SMF	Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; M. Grasshoff
UCR	University of California, Riverside, United States; S. I. Frommer
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; J. Coddington
WS	W. Shear
ZMB	Zoologisches Museum der Humboldt Universität, Berlin, Germany; M. Moritz
ZMK	Zoologisk Museum, København, Denmark; H. Enghoff
ZSM	Zoologische Staatssammlung, Munich, Germany

Numerous colleagues have provided specimens, natural history information, geographic data, maps, and other information: L. Avilés, R. L. Baptista, F. Coyle, A. Dean, W. Eberhard, J. Kochalka, R. Leech, A. Lopez, W. Maddison, E. A. Maury, H.-G. Müller, J. Palmer and D. Smith, V. Roth, W. C. Sedgwick, M. A. Serna D., H. Sturm, S. Williams. C. Valderrama A. sent specimens and maps of Colombia; J. Kochalka, natural history observations; H. Höfer, specimens and photographs; P. G. Aguilar, large maps of Peru; and L. Avilés, a map of Ecuador. H. D. Cameron gave valuable advice on the use of Latin.

D. Woessner skillfully did the word processing, and W. and D. Maddison solved numerous computer problems. L. Leibensperger sorted incoming specimens and assisted in all phases of the revision including the mounting of the illustrations. L. Levi and D. Woessner reworded some of the writing. P. Sierwald and the editor, F. Boisse-Kilgo, made useful suggestions. To all of the above I express my sincere thanks.

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METHODS

Araneus was one of the most difficult North American genera to revise, especially the small species. I was confronted with numerous different species of females, and could not at first separate the male specimens. It turned out that, for males, the most stable character was the shape of the hidden embolus, while the easy-to-see median apophysis varies within species, or may be similar in different species (Levi, 1971, 1973).

Neotropical *Araneus*, especially the similar-sized species of eastern Brazil and some others, are equally difficult. In males of three or four species, the most prominent feature, the palpal median apophysis, is similar in shape. Nearly identical males accompanied females of various species on the rare occasions they were collected with females. (Being found in a vial with a female never guarantees a correct match.) Not even the shape of the embolus cap and embolus permit clear separation. Do the species interbreed? Are the males identical? Finally, features of the subterminal apophysis, and the embolus and its lamella were found that permitted separation of the males. Unfortunately, the subterminal apophysis is difficult to study; black and heavily sclerotized, its features are not easily seen. The embolus lies behind the conductor and is often hidden. Subterminal apophysis sculpturing and embolus are seen only by careful examination, preferably of just-molted males, or on a black background with reflected light under high power. Other difficulties arose with females of *A. bogotensis,* from the Andes mountains. Some populations are more or less isolated from others and show remarkable variation. Individual females

may differ from each other more than from females of different species, but, in large collections, females with intermediate characters are always found. All the difficult specimens come from mountains of southern Colombia and northern Ecuador. Another puzzling species is *A. expletus*. No two specimens are quite the same. Only larger collections from Central America will determine whether all specimens here placed in *A. expletus* actually belong to the same species.

The Neotropical *Araneus* species can be separated neither by body shape, nor usually by color, pattern, and size (with very few exceptions, e.g., *A. venatrix*, *A. guttata*).

While it might be possible to separate species by molecular methods, it is not permissible to grind up collections from various museums or take tissue samples. In any case, the results would not be useful to ecologists who need to determine their specimens in the field.

The morphometric methods currently in vogue would require measurements of leg length, macrosetae counts, and eye ratios (see *Araneus meropes* below). However, in *Araneus,* leg length and eye ratios of both males and females are variable. Also in *Araneus,* many specimens have regenerated legs, which are slightly shorter than the originals. We tried macrosetae counts of the second leg of males when I first started araneid revisions. It was not successful (Berman and Levi, 1971; Carmichael, 1973). In *Araneus,* features of the genitalic structures are critical for separation of species, and even here there are difficulties. Lacking a practical way to convert the three dimensional sclerites of genitalic structures (e.g., texture of subterminal apophyses of palpi) into numbers, illustrations will have to be sufficient. Fortunately carefully-made illustrations have proved to be well suited for separation of species.

A dilemma should be mentioned: whether to take apart the genitalia of a rare holotype to improve description, or leave them undamaged in the hope easier characters will be found.

To make some of the illustrations of palpal parts, embolus, and subterminal apophysis, the palpi were not expanded. Instead I pulled the distal part of the palpus out with needles and on rare occasions removed the conductor.

Living individuals of *Araneus* species have green and red colors, pigments that readily dissolve in alcohol. Colors reported in descriptions are those of alcohol-preserved specimens unless otherwise stated.

Eye sizes were measured by comparing their diameter in profile with that of the anterior median eyes. Their distance from each other of the anterior row was measured by the diameter of the anterior median eyes in profile, from each other of the posterior row by the diameter of the posterior median eyes.

I am skeptical of many localities. The original label may have been misspelled or the locality name changed. Copying the collecting label when sorting may have produced further misspellings. There are obscure abbreviations of many old localities. (In the MCZ, one specimen of *A. trifolium,* common in Massachusetts, was allegedly collected in Fazenda de Secretario Vassouras, Rio de Janeiro, April 1871, by B. P. Mann.) Also, distributions are incomplete as many Neotropical areas have not been collected. It is characteristic of sporadic collecting that the only record of the common *A. venatrix* in Venezuela comes from a difficult-to-reach and out-of-the-way location, Sierra de la Neblina.

Araneus Clerck, 1758

Araneus Clerck, 1758: 15. Type species *A. angulatus* Clerck, 1758 (see comment in Levi, 1971: 133 and note below).

Aranea Linnaeus, 1758: 619. Type species *A. diadema* Linnaeus.

Epeira Walckenaer, 1805: 53. Type species designated by Latreille, 1810: 424. *Aranea diadema* Linnaeus.

Atea C. L. Koch, 1837: 3. Type species *Epeira sturmi* (Hahn) designated by Bonnet, 1955: 769.

Neopora Simon, 1864: 261. Type species *Aranea diadema* Linnaeus.

[illegible]sia [illegible] 1894: 182. Type species *Epeira corticaria* Emerton, designated by Levi, 1971: 133 (as subgenus).

Neosconella F. P.-Cambridge, 1904: 474. Type species by original designation *Neosconella styligera* F. P.-Cambridge.

?*Epeirella* Mello-Leitão, 1941a: 149. The type species by original designation is *Epeirella tucumana* Mello-Leitão with immature holotype [= ?*Araneus vincibilis*].

Amamrotypus Archer, 1951a: 17. Type species by original designation *Amamrotypus mammatus* Archer, 1951.

Euaranea Archer, 1951a: 34. Type species by original designation *Epeira cavatica* Keyserling (as subgenus).

Cambridgepeira Archer, 1951b: 2. Type species by original designation *Epeira detrimentosa* O. P.-Cambridge.

Conaranea Archer, 1951b: 5. Type species by original designation *Epeira excelsa* Banks [= *A. bispinosus* (Keyserling)].

Mimaranea Archer, 1951b: 7. Type species by original designation *Aranea triguttata* Fabricius. Named as subgenus of *Conaranea*.

Conepeira Archer, 1951b: 12. Type species by original designation *Epeira miniata* Walckenaer.

Note. Although Clerck was published in 1757 (Victory and Cokendolpher, 1989), Art. 3 of the International Code of Zoological Nomenclature, third edition, assigns the arbitrary date 1 January 1758 and directs Clerck as having priority over Linnaeus's Systema Naturae, tenth edition.

Diagnosis. Females of *Araneus* can be separated from those of other genera by the subspherical to triangular, often hairy, abdomen, which frequently has a pair of anterior humps, and by the epigynum, which has an annulate scape attached to a base (Figs. 1, 2).

Males of *Araneus* are separated from those of other genera by the structure of the palpus: two patellar setae, a median apophysis with spines or hooks, an apomorphy, a conductor close behind sitting on the rim of the tegulum (without basal extension), and the presence of subterminal and terminal apophyses separated by a distal hematodocha from the embolus (Figs. 3, 4, 14). As far as is known, the embolus of a virgin male always has a cap, an apomorphy not found in related genera, which breaks off and lodges in the epigynum when mating (Figs. 77, 84). The cap is often seen attached to the epigynum of mated females (Figs. 435, 445, 466, 477), and may prevent a second mating with another male.

Description. The head of *Araneus* females is relatively narrow, the median eyes projecting anteriorly from the laterals. The lateral eyes tend to be smaller than the medians; the anterior or posterior median eyes are the largest. The carapace is usually covered by setae. The first leg is longer than the fourth. The abdomen is spherical to slightly wider than long, sometimes oval, often with a pair of anterior humps (Figs. 12, 442, 480). It usually is hairy in large species, but not so in the small ones.

The epigynum always has an annulate scape. (Only in *A. tigana* is the scape a fused sclerite without rings, Fig. 9.) The scape is attached to the base. Often (as in *A. bogotensis*) the scape is bent on itself, the spoon-shaped end directed posteriorly (Fig. 1). In only some species the scape is torn off, presumably by the male when mating (Fig. 10), preventing later matings with other males. In posterior view, there is a median plate (sclerite) framed by a lateral plate on each side (Fig. 2). The openings are usually ventral in the slit between median and lateral plates, rarely in a round depression.

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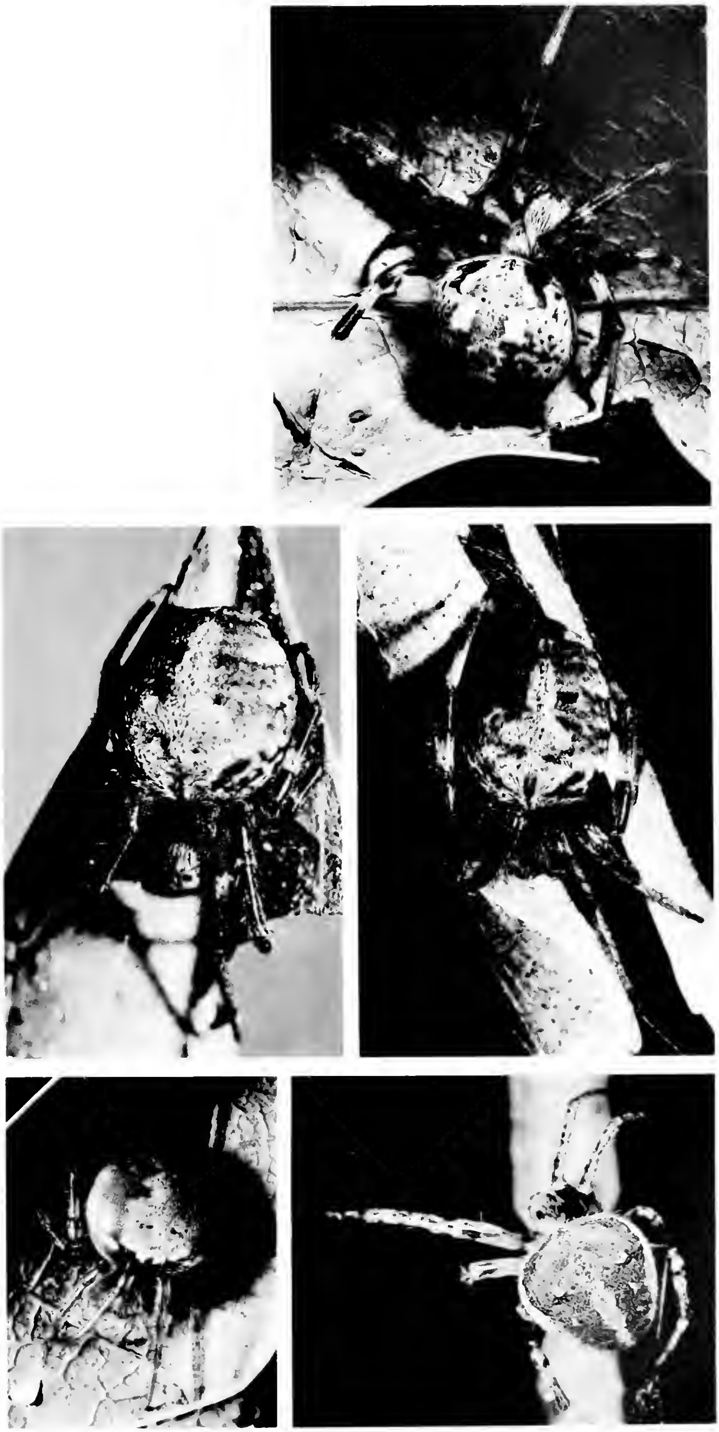
Plate 1. Upper row, *Araneus workmani*, carapace black with white hair, legs black on translucent white, median band of abdomen with purple-red spots, white patches to side, sides with black and brown marks. Total length 8 mm. Middle row left, *A. omnicolor*, carapace brownish black with white setae, legs black and translucent white, dorsum of abdomen with tiny red stipples, sides with olive, brown, and black. Total length 9 mm. Right, *A. vincibilis*, head black with white setae, legs black on translucent white, abdomen anterior with reddish spots in light area, orange-brown and black marks and some white on sides. Bottom row left, *A. unanimus*, carapace, legs, abdomen green, anterior black with yellowish outline and sides red. Total length 7 mm. Right, *A. urubamba*, carapace brown with white setae, legs brown on translucent white, abdomen dark olive-brown on beige, spots orange-brown. Total length 6.5 mm.



The male may be the same size or smaller than the female. The head is always narrower than that of the female. The endite usually has a tooth facing a similar tooth on the palpal femur. The legs are longer than those of the female. The first coxa has a hook on the rim. This hook is absent in the small species, rarely absent in larger ones. The second coxa may have a cone (*A. uniformis*). The coxae never have macrosetae. The second tibia is thicker than the first, usually with some short stout macrosetae. Some small species have the first tibia so modified. The males of some species have neither modified. In males the abdomen is usually oval, slightly pointed behind.

The palpal patella has two setae (*A. cohnae* has only one patellar seta). The palpal tibia in all *Araneus* species has a similar shape: it is conical, enlarged, and bulging on the lateral side when seen in ventral view (Figs. 14, 15). The cymbium of the palpus lacks a tarsal organ. The radix is a lobe of the tegulum (Figs. 3, 4), the median apophysis is the most distinctive feature, with spines on either end. (Unfortunately, its shape and its spines are not necessarily diagnostic for species, although it is useful in separating some otherwise similar species.) Right behind and lateral to the median apophysis is the conductor which sits on the rim of the tegulum. The conductor is white, sometimes sclerotized (in large Nearctic species), flexible, and may have a tooth on its base. In *Araneus*, the conductor never has an extension from its base (As in *Alpaida*, *Wixia*, or *Cyclosa*), and there is no paramedian apophysis. The embolus often has a lamella; embolus and lamella are usually hidden behind the conductor. The subterminal apophysis is usually a plate, often sculptured. The distal hematodocha separates the subterminal and terminal apophyses from each other and both from the embolus. The terminal apophysis may have small hooks or spines on its tip (Figs. 3, 4, 14). Palpi that have contracted after expanding may not move the terminal apophysis back into its position in the virgin palpus.

Species Diagnostic Features of Araneus. Females of related species generally can be distinguished by the plates in posterior view of the epigynum (Fig. 2). Males usually can be distinguished by the shape of the embolus (Fig. 3) (often hidden by the conductor) but some species have a distinctively shaped median apophysis. Unlike the hidden embolus, the median apophysis is easily seen. Also the sculpturing of the subterminal apophysis appears to be of importance. Because it is heavily sclerotized and black, the subterminal apophysis is also difficult to examine. For new species descriptions the ventral and posterior views of the epigynum have to be illustrated as well as the mesal view of the (left) palpus. Scanning electron micrographs of the terminal or dorsal aspect of palpi, or squashed mounts of the cleared epigynum showing internal ducts are not sufficient. (Both unfortunately are found in recent literature.) Species cannot be separated by the color pattern of the abdomen (exceptions here are *A. venatrix* and a few other species). Attempts to separate species by proportions or macrosetae count is wasting time (Berman and Levi, 1971; Carmichael, 1973; Levi, 1973). Also leg length appears quite variable within species and cannot be used to diagnose species, although it is useful information. *Araneus* specimens often have regenerated

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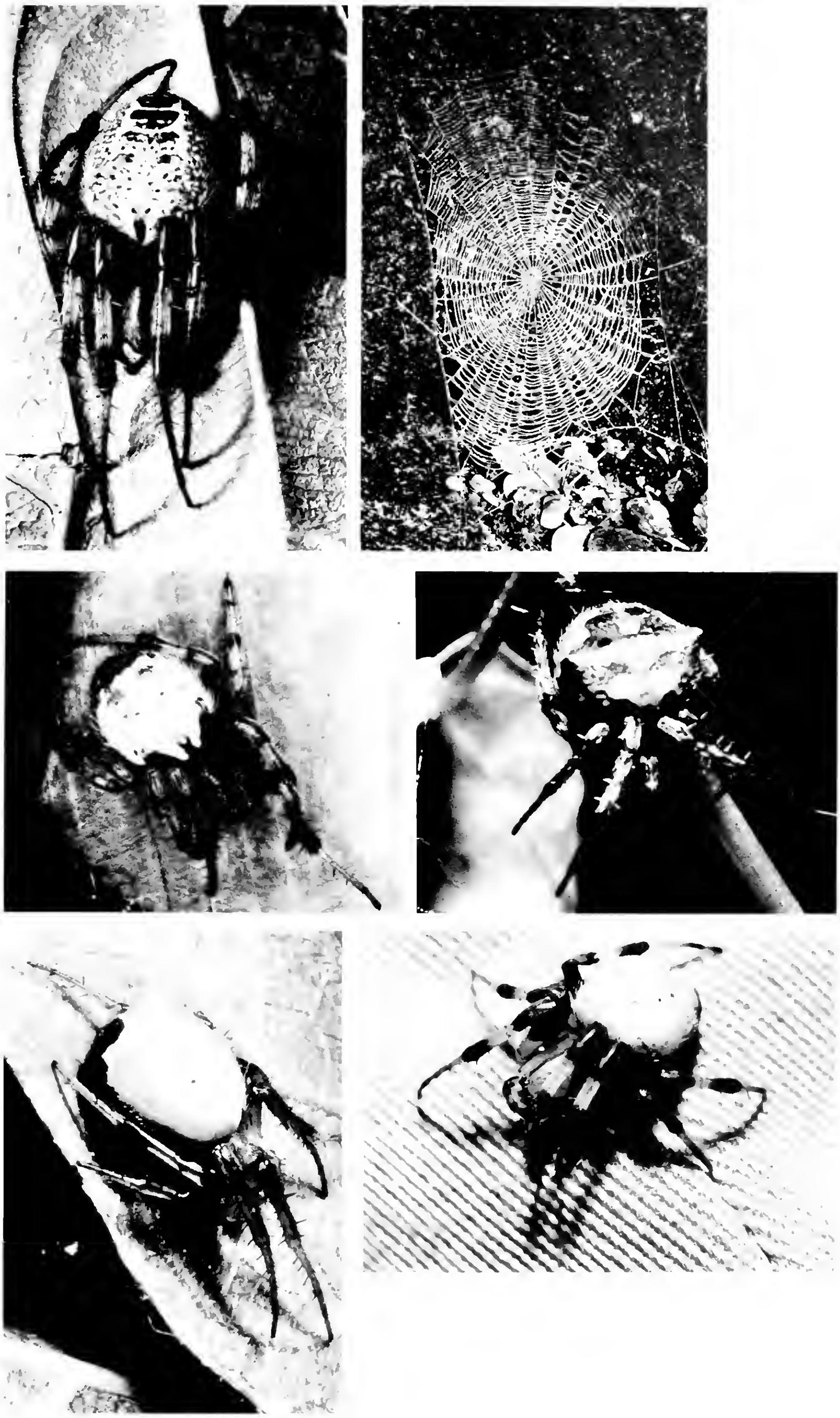
Plate 2 Upper row left, *Araneus venatrix* (Rio de Janeiro), carapace dark brown, legs red-brown and transparent white, abdomen with red and black spots, greenish-white on sides, posterior black transverse bars. Total length 12 mm. Right, web of *A. iguacu*, 11 cm horizontal diameter. Middle row left, *A. guttatus* (Panama), carapace black, legs black and brown, abdomen white with black marks. Total length 8 mm. Right, *A. iguacu*, legs black and translucent white, abdomen white with green patches and black marks. Total length 4.5 mm. Bottom row left, *A. tijuca*, carapace orange, legs dark orange and black, abdomen green, posterior black with white outline. Total length 6 mm. Right, *Dubiepeira dubitata*, carapace translucent white with a black line, legs black on transparent white, abdomen bright green. Total length 12 mm.



legs, which are smaller than non-regenerated legs.

Natural History. Large *Araneus* females make a retreat in a rolled leaf or in bark or lichens and have a signal line going to the center of the large orb web (Levi, 1971, 1973). Small species may inhabit tree crowns. Difficulty in collecting may be the reason for the rarity of many species in collections. Many species living in shrubs are easiest to collect by unrolling leaves. Males of all species are sometimes collected with females of a different species.

Relationship. Araneus is related to other araneid genera that have an annulate scape in the epigynum, that lack a paramedian apophysis, whose conductor sits on the rim of the tegulum behind the median apophysis, and that have a terminal and a subterminal apophyses. These genera include *Aculepeira* (which has a pointed scape and oval abdomen), *Kaira* (which has cauliflower-shaped structures on the abdomen), *Larinia* (which has an oval to elongate abdomen), *Metazygia* (which has a projecting club-shaped median apophysis), *Metepeira* (which has small male and female genitalia and a median apophysis with two flagella), *Nuctenea* (which has only a small hematodocha between terminal and subterminal apophysis, and an oval flattened abdomen), *Cercidia*, and others. The conductor of *Cercidia* is away from the rim. *Araneus* is not close to *Alpaida*, *Wixia*, *Eriophora*, *Molinaranea*, *Cyclosa*, and others that have a paramedian apophysis. (More on the relationships of araneid genera is in preparation.)

Within *Araneus*, the species that have two spines on the proximal end of the median apophysis (Figs. 3, 10) are the primitive ones, as semblance of this shape is found in other genera: *Aculepeira*, modified in *Metepeira*, *Kaira*, and *Larinia*. The greatest diversity of the median apophysis is found in the many small species, which probably evolved from larger ancestors. The many large Neotropical species are also very similar and perhaps closer to *Araneus marmoreus* Clerck because of the similarly shaped median apophysis. The large Nearctic species are more specialized than the larger Neotropical species, judging by the often sclerotized, modified conductor and diversity in the shape of the median apophysis. The epigynum of *Araneus marmoreus* has basal lamellae not found in South American species. But indication of such lamellae are found in some large individuals of species that otherwise do not have this structure. As in the larger South American species, *A. marmoreus* has an embollar lamella (Levi, 1971, fig. 6).

I have been unable to find good characters other than size that split off the group of many small species. As is characteristic in spiders and perhaps other animals, the tiny species show a greater diversity in body shape and genitalia. The two small species *A. sturmi* (Hahn), *A. triguttatus* (Fabricius) found in Europe are often placed in the genus *Atea*.

Distribution. Araneus species are mainly Holarctic, but may be found world-wide except perhaps in Australia and New Zealand. The species described from Africa, south of the Sahara, all may belong to other genera (personal communication M. Grasshoff).

Most *Araneus* species are Nearctic and Central American (Map 1). Next in showing an abundance of species are eastern Brazil and the Andes (Map 1). Related species have often similar distributions (e.g., the large species of eastern Brazil, the species found in Chile, and *A. venatrix*, *A. guttatus*). The greatest diversity in structure of genitalia and appearance is found among the small species of Mexico and Central America, most similar are the species of southern South America.

Misplaced and Unrecognizable Neotropical Species

The correct placement of *Araneus* nominal species that do not belong in *Araneus* (or in *Dubiepeira* or *Aculepeira*) is provided in the two lists below. (The lists were prepared from the catalogs of Roewer, 1942, and Brignoli, 1983.) The literature citations for these names can be found in the catalogs and are not repeated here.

Many misplaced species belong in unnamed, new genera. They will be named in future papers. The names of some misplaced species may be junior synonyms of older names.

Misplaced Species

Acrosoma transitoria C. L. Koch, 1839: 119, pl. 518, ♀; belongs in *Wagneriana*.
Acrosoma tumida Taczanowski, 1879: 120, pl. 1, fig. 34, ♀; belongs in *Wixia*.
Aranea bicolorata Roewer, 1942: 837, new name for *Epeira bicolor* C. L. Koch, 1839, preoccupied by *Epeira bicolor* Walckenaer, 1802; is a *Parawixia*.
Aranea citrinella Roewer, 1942: 839, new name for *Epeira citrina* Keyserling, 1892, erroneously thought by Roewer to be preoccupied by *Aranea citrina* Fourcroy, 1785 = *Alpaida citrina*.
Aranea coniformis Roewer, 1942: 839, new name for *Alpaida conica* O. P.-Cambridge, 1889, erroneously thought by Roewer to be preoccupied by *Aranea conica* Pallas, 1772 = *Alpaida conica*.
Aranea cylindriformis Roewer, 1942: 840, new name for *Epeira cylindrica* O. P.-Cambridge, 1889, preoccupied by *Epeira cylindrica* Taczanowski, 1878; is a linyphiid.
Aranea dilatata F. P.-Cambridge, 1904: 513, pl. 49, fig. 9, ♂; belongs in *Metazygia*.
Aranea errans Roewer, 1942: 841, new name for *Epeira erratica* Keyserling, 1883, erroneously thought by Roewer to be preoccupied by *Aranea erratica* Olivier, 1789; is a *Bertrana*.
Aranea fiebrigi Dahl, 1906: 735; belongs in *Wixia*.
Aranea gracilenta Roewer, 1942: 843, new name for *Epeira gracilis* Keyserling, 1865, preoccupied by *Epeira gracilis* Walckenaer, 1805 = *Argiope argentata* (Fabricius). NEW SYNONYMY.
Aranea hirtipedata Roewer, 1942: 844, new name for *Epeira hirtipes* Taczanowski, 1878, erroneously thought by Roewer to be preoccupied by *Aranea hirtipes* Fabricius, 1775; belongs in *Mangora*.
Aranea latro Fabricius, 1775: 412 = *Alpaida latro*.
Aranea mundulella Strand, 1915: 114; belongs in *Metazygia*.
Aranea nigrocincta F. P.-Cambridge, 1904: 513, pl. 49, figs. 11, 12, ♀, ♂; belongs in an unnamed genus.
Aranea nigropunctatula Roewer, 1942: 848, new name for *Epeira nigropunctata* Taczanowski, 1878, preoccupied by *Epeira nigropunctata* L. Koch, 1871 = *Alpaida calotypa* (Chamberlin).
Aranea ocellatula Roewer, 1942: 849, new name for *Epeira ocellata* O. P.-Cambridge, 1889: 29, erroneously thought by Roewer to be preoccupied by *Aranea ocellata* Linn., 1758. The type is an early instar, probably of *Eriophora ravilla* (C. L. Koch).
Aranea orina Chamberlin, 1916: 248, pl. 4, fig. 3, ♂; belongs in *Eustala*.
Aranea roemeri Strand, 1908: 3 = *Alpaida roemeri*.

Map 1. Approximate number of species of *Araneus* in different areas.

Aranea santa Chamberlin, 1916: 254, pl. 19, fig. 10, ♀; belongs in *Metepeira*.
Aranea tatarendensis Tullgren, 1905: 34, pl. 5, fig. 12, ♀ = *Wixia tatarendensis* (Tullgren). NEW COMBINATION.
Aranea trisignata Roewer, 1942: 854, new name for *Epeira trilineata* Taczanowski, 1878: 162, erroneously thought by Roewer to be preoccupied by *Aranea trilineata* Linn., 1767 = *Alpaida trilineata*.
Aranea viridipedata Roewer, 1942: 856, new name for *Epeira viridipes* Taczanowski, 1878: 155, preoccupied by *Epeira viridipes* Doleschall, 1859; belongs in *Eustala*.
Araneus acacesiiformis di Caporiacco, 1954: 108, fig. 27, ♀; is an immature *Eriophora nephiloides* (O. P.-Cambridge). NEW SYNONYMY.
Araneus akeholmi Brignoli, 1983: 262, new name for *A. holmi* di Caporiacco, 1955, preoccupied by *Araneus holmi* Schenkel, 1953; is *Wixia tatarendensis* (Tullgren). NEW SYNONYMY.
Araneus albisecta Mello-Leitão, 1936: 127, pl. 15, ♀; belongs in *Molinaranea*.
Araneus argyronotus Mello-Leitão, 1939: 111; is an immature *Eriophora edax* (Blackwall). NEW SYNONYMY.
Araneus aysenensis Tullgren, 1902: 32, pl. 3, fig. 4, ♀; belongs in *Molinaranea*.
Araneus borellii Simon, 1897: 6 = *Alpaida veniliae* (Keyserling).
Araneus calotypa Chamberlin, 1916: 256, pl. 19, fig. 4, ♂ = *Alpaida calotypa*.
Araneus carteri Badcock, 1932: 25, fig. 17; ♀, ♂ = *Alpaida alticeps* (Keyserling).
Araneus castaneoscutatus Simon, 1895: 806; belongs in *Metazygia*.
Araneus collusor Petrunkevitch, 1911: 285, new name for *Heterognatha chilensis* Nicolet, 1849, errone-

ously thought by Petrunkevitch to be preoccupied by *Epeira chilensis* Nicolet, 1849; belongs in *Heterognatha*, probably Mimetidae.

Araneus compsa Chamberlin, 1916: 252, pl. 19, fig. 6, ♀; belongs in *Metepeira*.

Araneus cylicophorus Badcock, 1932: 26, fig. 18, ♀; belongs in *Verrucosa*.

Araneus cyrtophoroides F. P.-Cambridge, 1904: 518, pl. 51, fig. 4, ♀ = *Cyrtophora nympha* Simon. NEW SYNONYMY.

Araneus designatus Chamberlin and Ivie, 1936: 51, pl. 14, figs. 126, 127, ♀; is an immature *Alpaida bicornuta* (Taczanowski).

Araneus duocypha Chamberlin, 1916: 256, pl. 18, figs. 8–10, ♀; the holotype is probably a *Wixia*.

Araneus eriophoroides di Caporiacco, 1954: 111, fig. 29, ♂. Type lost (not in MNHN, MZUF); belongs in *Parawixia*.

Araneus flavosellata Simon, 1895: 824. No specimen with this name in MNHN. It might be *Bertrana flavosellata* Simon, 1893: 326.

Araneus fuligineus rhomboidalis Franganillo Balboa, 1930 = ?*Eriophora ravilla* (C. L. Koch).

Araneus fuligineus sanguineus Franganillo Balboa, 1930 = ?*Eriophora ravilla* (C. L. Koch).

Araneus globigera Hogg, 1913: 39, pl. 1, fig. 4, ♂; belongs in *Molinaranea*.

Araneus holmi di Caporiacco, 1955: 354; is *Wixia tatarendensis* (Tullgren). NEW SYNONYMY.

Araneus inexplicabilis Badcock, 1932: 38, fig. 16, ♀ = *Alpaida rubellula* (Keyserling).

Araneus mammifera Tullgren, 1902: 34, pl. 3, fig. 5, ♀; belongs in *Molinaranea*.

Araneus manicatus Simon, 1895: 822 = *Alpaida manicata*.

Araneus moatus Chamberlin and Ivie, 1936: 47, pl. 14, fig. 125 = *Alpaida moata*.

Araneus multipunctatus Simon, 1895: 815 = *Alpaida tabula* (Simon).

Araneus mutata Chamberlin and Ivie, 1936: 46, pl. 14, figs. 128, 129, ♀ = *Alpaida truncata* (Keyserling).

Araneus neotheis Petrunkevitch, 1911: 305, for *Epeira theisii*:—Keyserling, 1893, misidentification = *Neoscona moreli* (Vinson).

Araneus nigrofrenata Simon, 1895: 816 = *Alpaida nigrofrenata*.

Araneus nigrolineatus di Caporiacco, 1955: 357, fig. 263, ♀; belongs in *Acacesia*.

Araneus nordenskjöldii Tullgren, 1905: 29, pl. 3, fig. 9, pl. 4, fig. 9, ♀, ♂; belongs in *Parawixia*.

Araneus paraopeba Mello-Leitão, 1917: 92, fig. 10, ♀, belongs in *Parawixia*.

Araneus patagonica Tullgren, 1901: 218; belongs in *Molinaranea*.

Araneus perperus Petrunkevitch, 1911: 309, new name for *Epeira perplexa* Banks, 1898: 251, preoccupied by *Epeira perplexa* Walckenaer, 1842 = *Carepalxis perpera*. NEW COMBINATION.

Araneus phaetontis Simon, 1896: 67; belongs in *Molinaranea*.

Araneus quadriloratus Simon, 1897: 5 = *Alpaida quadrilorata*.

Araneus ribeiroi Mello-Leitão, 1917: 89; belongs in *Parawixia*.

Araneus riveti Berland, 1913: 92, pl. 9, figs. 42, 43, ♀. Holotype lost (not in MNHN); belongs in an unnamed genus.

Araneus rugosa Badcock, 1932: 24; belongs in *Parawixia*.

Araneus sandrei Simon, 1895: 816 = *Alpaida sandrei*.

Araneus sermonifera Mello-Leitão, 1932: 124, new name for *Araneus socialis*:—Burmeister, 1872: 492, misidentification; belongs in *Parawixia*.

Araneus setospinosa Chamberlin and Ivie, 1936: 48, pl. 14, fig. 124, ♀ = *Cyrtophora nympha* Simon. NEW SYNONYMY.

Araneus surculorum Simon, 1896: 67; belongs in *Molinaranea*.

Araneus tabula Simon, 1895: 815, fig. 867, ♀ = *Alpaida tabula*.

Araneus taczanowskii Simon, 1896: 473 = *Alpaida delicata* (Keyserling).

Araneus trigonellus di Caporiacco, 1954: 107, fig. 26, ♀; belongs in *Wixia*.

Araneus trinitatis Hogg, 1918: 166; belongs in *Eustala*.

Araneus tristimoniae Petrunkevitch, 1911: 320, new name for *Epeira tristis* Taczanowski, 1873: 131, preoccupied by *Epeira tristis* Blackwall, 1862 = *Neoscona nautica* (L. Koch).

Araneus tuonabo Chamberlin and Ivie, 1936: 50, pl. 14, fig. 1230, ♀ = *Alpaida tuonabo*.

Araneus vallentini Hogg, 1913: 37, pl. 1, fig. 3, ♀; belongs in *Molinaranea*.

Araneus wenzeli Simon, 1897: 874 = *Alpaida wenzeli*.

Araniella geayi di Caporiacco, 1954: 104, fig. 24, ♀; is an immature *Eriophora edax* (Blackwall).

Atea lewisi Archer, 1958: 17, figs. 39, 40, ♀; belongs in an unnamed genus.

Epeira acuta Keyserling, 1965: 816, pl. 18, figs. 13, 14, ♀ = *Alpaida acuta*.

Epeira adiantoides Taczanowski, 1878: 148, pl. 1, fig. 4, ♀, ♂ = *Neoscona oaxacensis* (Keyserling).

Epeira aestimabilis Keyserling, 1892: 181, pl. 9, fig. 133, ♀, ♂ = *Alpaida championi* O. P.-Cambridge.

Epeira albiventer Keyserling, 1884: 651, pl. 21, fig. 3, ♀; belongs in *Eustala*.

Epeira bicolor C. L. Koch, 1839: 57, pl. 374, ♀; preoccupied by Walckenaer, 1802; is a *Parawixia*.

Epeira bicornuta Taczanowski, 1878: 168, pl. 2, fig. 18, ♀, ♂ = *Alpaida bicornuta*.

Epeira carminea Taczanowski, 1878: 163, pl. 2, fig. 14, ♀ = *Alpaida carminea*.

Epeira caudacuta Taczanowski, 1873: 136, pl. 5, fig. 16, ♀; belongs in *Mecynometa*.

Epeira championi O. P.-Cambridge, 1889: 42, pl. 5, figs. 12, 13, ♀, ♂ = *Alpaida championi*.

Epeira chilensis Nicolet, 1849: 487; belongs in *Molinaranea*.

Epeira cinaberina Nicolet, 1849: 490, pl. 5, fig. 9, ♀; belongs in *Molinaranea*.
Epeira citrina Keyserling, 1892: 88, pl. 4, fig. 66, ♀ = *Alpaida citrina*.
Epeira clymene Nicolet, 1849: 503; belongs in *Molinaranea*.
Epeira consequa O. P.-Cambridge, 1889: 36; belongs in *Wixia*.
Epeira cooksonii Butler, 1877: 76, pl. 13, fig. 2, ♀ = *Neoscona oaxacensis* (Keyserling).
Epeira coronigera Taczanowski, 1878: 157, pl. 1, fig. 9, ♀; belongs in *Parawixia*.
Epeira cylindrica O. P.-Cambridge, 1889: 19, pl. 7, figs. 12, 13, ♀, ♂; preoccupied by Taczanowski, 1878; is a linyphiid.
Epeira davisi Hingston, 1932: 365 = *Cyrtophora guianensis* (Keyserling). NEW SYNONYMY.
Epeira delicata Keyserling, 1892: 183, pl. 9, fig. 135, ♀, ♂ = *Alpaida delicata*.
Epeira deliciosa Keyserling, 1893: 234, pl. 11, fig. 174, ♀, ♂ = *Alpaida carminea* Taczanowski, 1878.
Epeira destricta O. P.-Cambridge, 1889: 39, pl. 4, fig. 14; belongs in *Wixia*.
Epeira dubia Keyserling, 1863: 123, pl. 4, figs. 12, 13, ♀; belongs in *Metazygia*.
Epeira electa Keyserling, 1883: 196, pl. 16, fig. 2, ♂; belongs in *Kaira*.
Epeira elinguis Keyserling, 1883: 198, pl. 15, fig. 4, ♀; belongs in *Bertrana*.
Epeira erratica Keyserling, 1883: 197, pl. 15, fig. 3, ♀; belongs in *Bertrana*.
Epeira erudita Nicolet, 1849: 504; belongs in *Molinaranea*.
Epeira essequibensis Hingston, 1932: 366; belongs in *Wixia*.
Epeira flaviventris Nicolet, 1849: 494; belongs in *Molinaranea*.
Epeira floridensis Banks, 1904: 129, pl. 7, fig. 5, ♀ = *Araneus miniatus* (Walckenaer).
Epeira fuliginea C. L. Koch, 1839: 58, pl. 375, ♀ = *Eriophora fuliginea*.
Epeira galatheae Thorell, 1891: 53; belongs in *Metepeira*.
Epeira genialis Keyserling, 1892: 156, pl. 8, fig. 114, ♀; belongs in *Metazygia*.
Epeira glomerabilis Keyserling, 1892: 154, pl. 8, fig. 113, ♀, ♂; belongs in *Metazygia*.
Epeira gracilis Keyserling, 1865: 826, pl. 19, figs. 29, 30, ♂, preoccupied by Walckenaer, 1805 = *Argiope argentata* (Fabricius). NEW SYNONYMY.
Epeira graphica O. P.-Cambridge, 1889: 22, pl. 7, fig. 16, ♂ = *Alpaida graphica*.
Epeira grayii Blackwall, 1863: 34, = *Alpaida grayi*.
Epeira gressa Keyserling, 1892: 166, pl. 8, fig. 123, ♀; belongs in *Metepeira*.
Epeira gundlachi Banks, 1914: 641, pl. 43, fig. 8, ♀; probably belongs in *Larinia*.
Epeira helvola O. P.-Cambridge, 1889: 24, pl. 5, figs. 1, 2, ♀, ♂; belongs in *Metazygia*.
Epeira hirtipes Taczanowski, 1878: 164, pl. 2, fig. 15, ♀, ♂; belongs in *Mangora*.
Epeira hispida C. L. Koch, 1845: 889 = *Eriophora fuliginea* (C. L. Koch). NEW SYNONYMY.
Epeira hispida Nicolet, 1849: 505; belongs in *Molinaranea*.
Epeira hyadesi Simon, 1884: 121, pl. 3, figs. 5, 6, ♀; belongs in an unnamed genus.
Epeira incerta O. P.-Cambridge, 1889: 23, pl. 4, fig. 15, ♀; belongs in *Metazygia*.
Epeira inflata Nicolet, 1849: 504; belongs in *Molinaranea*.
Epeira jelskii Taczanowski, 1873: 139, pl. 5, fig. 17, ♀, ♂; belongs in *Wagneriana*.
Epeira kochii Taczanowski, 1873: 134; is probably a *Parawixia*.
Epeira lamentaria Keyserling, 1883: 199; belongs in an unnamed genus.
Epeira laticeps O. P.-Cambridge, 1889: 18, pl. 4, fig. 16, ♀; belongs in an unnamed genus close to *Metazygia*.
Epeira messalina Hasselt, 1888: 181, pl. 6, figs. 1, 2, ♀ = *Eriophora fuliginea* (C. L. Koch).
Epeira minas Keyserling, 1892: 95, pl. 5, fig. 71, ♀, ♂; belongs in *Parawixia*.
Epeira monticola Keyserling, 1892: 94, pl. 4, fig. 70, ♀; belongs in *Parawixia*.
Epeira musiva Hasselt, 1889: 184, pl. 5, figs. 5–7, ♀ = *Eriophora nephiloides* (O. P.-Cambridge). NEW SYNONYMY.
Epeira nicaraguensis Keyserling, 1885: 532, pl. 13, fig. 31, ♀ = *Eriophora ravilla* (C. L. Koch).
Epeira nigrata Nicolet, 1849: 504; belongs in *Molinaranea*.
Epeira nigriventris Taczanowski, 1878: 151, pl. 1, fig. 6, ♀, ♂; belongs in *Metepeira*.
Epeira nigropunctata Taczanowski, 1878: 167, pl. 2, fig. 17, ♀, ♂, preoccupied by L. Koch, 1871 = *Alpaida calotypa* (Chamberlin).
Epeira nigropustulata O. P.-Cambridge, 1893: 111, pl. 15, fig. 5 = *Alpaida truncata* (Keyserling).
Epeira ocellata O. P.-Cambridge, 1889: 29. The type is an early instar, probably of *Eriophora ravilla* (C. L. Koch).
Epeira pallidula Keyserling, 1863: 124, pl. 4, figs. 14, 15, ♀; belongs in *Metazygia*.
Epeira pantherina Taczanowski, 1872: 132 = *Alpaida veniliae* (Keyserling).
Epeira perplexa Banks, 1898: 251, preoccupied by Walckenaer, 1842; belongs in *Carepalxis*.
Epeira punctipes Taczanowski, 1878: 166, pl. 2, fig. 16, ♀; belongs in *Mangora*.
Epeira reptilis Keyserling, 1892: 244, pl. 12, fig. 182, ♂ = *Araneus pratensis* Emerton.
Epeira rhodomelas Taczanowski, 1878: 147, pl. 1, fig. 3, ♀ = *Alpaida acuta* (Keyserling).
Epeira rivalis Keyserling, 1892: 103, pl. 5, fig. 76, ♀. Holotype lost (not in BMNH, USNM); probably belongs in *Parawixia*.
Epeira rostrata Keyserling, 1893: 230, pl. 11, fig. 171, ♀; belongs in *Mangora*.
Epeira rostratula Keyserling, 1892: 82, pl. 4, fig. 62, ♂ = *Alpaida rostratula*.

Epeira rubellula Keyserling, 1892: 81, pl. 4, fig. 61, ♀ = *Alpaida rubellula*.

Epeira salei Keyserling, 1863: 93, pl. 4, figs. 10, 11, ♀, belongs in *Metepeira*.

Epeira seditiosa Keyserling, 1893: 212, pl. 10, fig. 157, ♂; belongs in *Metepeira*.

Epeira septemmammata O. P.-Cambridge, 1889: 42, pl. 7, fig. 6, ♀ = *Alpaida septemmammata*.

Epeira simplicissima Keyserling, 1883: 203, pl. 15, fig. 8, ♀; belongs in *Metazygia*.

Epeira singularis Banks, 1898: 252, pl. 15, fig. 4, ♀ = *Neoscona arabesca* (Walckenaer).

Epeira spinigera O. P.-Cambridge, 1889: 43, pl. 5, figs. 9, 10, ♀ = *Alpaida bicornuta* (Taczanowski).

Epeira spinosa Taczanowski, 1873: 141, pl. 5, fig. 18, ♀, ♂; belongs in *Wagneriana*.

Epeira strenua Keyserling, 1893: 257; belongs in *Mangora*.

Epeira thalia Nicolet, 1849: 503; belongs in *Molinaranea*.

Epeira theisii:—Keyserling, 1893: 246, pl. 12, fig. 184, ♀, misidentification = *Neoscona morela* (Vinson).

Epeira trapezoides Karsch, 1879: 107 = *Eriophora fuliginea* (C. L. Koch).

Epeira trilineata Taczanowski, 1878: 162, pl. 2, fig. 13, ♀ = *Alpaida trilineata*.

Epeira trispinosa Keyserling, 1892: 78, pl. 4, fig. 59, ♀, ♂ = *Alpaida trispinosa*.

Epeira tristis Taczanowski, 1873: 131, preoccupied by Blackwall, 1862 = *Neoscona nautica* (L. Koch).

Epeira tubulifaciens Hingston, 1932: 366; belongs in *Spilasma*.

Epeira unguiformis Keyserling, 1893: 237, pl. 11, fig. 177, ♀ = *Alpaida veniliae* (Keyserling).

Epeira ursina Keyserling, 1865: 822, pl. 19, figs. 3–5, ♀ = *Eriophora fuliginea* (C. L. Koch).

Epeira variabilis Keyserling, 1863: 126, pl. 6, figs. 1–4, ♀, ♂ = *Alpaida variabilis*.

Epeira velutina Taczanowski, 1878: 159, pl. 1, fig. 10, ♀; belongs in *Parawixia*.

Epeira veniliae Keyserling, 1865: 817, pl. 19, fig. 23, ♀, ♂ = *Alpaida veniliae*.

Epeira venustula Keyserling, 1879: 308, pl. 4, fig. 11, ♀, ♂; belongs in *Wixia*.

Epeira verecunda Keyserling, 1865: 824, pl. 19, figs. 14–16, ♀, ♂; is probably a *Wixia*. (Both palpi lost from type specimen.)

Epeira vigilax Keyserling, 1893: 211, pl. 10, fig. 156, ♂, belongs in *Metepeira*.

Epeira viridipes Taczanowski, 1878: 155, pl. 1, fig. 8, ♀, ♂, belongs in *Eustala*.

Epeira variosa Keyserling, 1892: 165, pl. 8, fig. 122, ♀, belongs in an unnamed genus.

Epeira voluptifica Keyserling, 1892: 152, pl. 7, fig. 112, ♀, ♂, belongs in *Metazygia*.

Epeira zelotypa Keyserling, 1883: 202, pl. 15, fig. 7, ♀ = *Chrysometa zelotypa*.

Epeira zilloides Banks, 1898: 255, pl. 15, fig. 2, ♀, ♂; belongs in *Metazygia*.

Epeirella albocincta Mello-Leitão, 1948: 169, fig. 11, ♂ = *Alpaida albocincta*.

Epeiroides albonotatus Mello-Leitão, 1945: 237; is *Alpaida truncata* (Keyserling.)

Epeiroides bahiensis Keyserling, 1885: 524, pl. 13, fig. 23, ♀; stays in original genus *Epeiroides*.

Epeiroides fasciolata O. P.-Cambridge, 1889: 15, pl. 8, fig. 5, ♂; belongs in *Mastophora*.

Epeiroides lamprus Soares and Camargo, 1948: 370, figs. 23, 24, ♀; belongs in *Verrucosa*.

Heterognatha chilensis Nicolet, 1849: 470, pl. 5, fig. 3, ♀; probably belongs in Mimetidae.

Heterognatha margaritacea Nicolet, 1849: 471; probably belongs in Mimetidae.

Mahadeva undulata Keyserling, 1892: 67, pl. 3, fig. 52, ♀; belongs in *Parawixia*.

Mahadeva zebra Keyserling, 1892: 68, pl. 3, fig. 53, ♀ = *Verrucosa zebra*. NEW COMBINATION.

Molinaranea setosa Mello-Leitão, 1948: 169; belongs in *Parawixia*.

Neoscona conifera F. P.-Cambridge, 1904: 409, pl. 44, figs. 6, 7, ♀, ♂ = *Neoscona oaxacensis* (Keyserling).

Neoscona minima F. P.-Cambridge, 1904: 471, pl. 44, figs. 11, 12 = *Neoscona arabesca* (Walckenaer).

Tricantha albopunctata Taczanowski, 1879: 123; belongs in *Wixia*.

Unrecognizable Names

The unrecognizable names are those of species described by Walckenaer, Nicolet, Blackwall, Franganillo, early Mello-Leitão, and Hingston, authors who did not illustrate the genitalia of the species they named, and did not leave well-marked specimens in a museum. These same authors made inadvertent homonyms which were subsequently replaced by Petrunkevitch (1911), Roewer (1942), and Brignoli (1983) in their catalogs. Thus, a number of these doubtful nominal species have two names. Also included here are some names of other authors whose types have been lost.

Aranea affinitata Roewer, 1942: 836, new name for *Epeira affinis* Nicolet, 1849, preoccupied by *E. affinis* Blackwall, 1846.

Aranea crux Roewer, 1942: 840, new name for *Epeira cruciata* Nicolet, 1849, preoccupied by *E. cruciata* Walckenaer, 1805.

Aranea depressata Roewer, 1942: 841, new name for *Epeira depressa* Walckenaer, 1841, erroneously thought by Roewer to be preoccupied by *Aranea depressa* Razoumowsky, 1789.

Aranea dorsatula Roewer, 1942: 841, new name for

Epeira dorsalis Nicolet, 1849, erroneously thought by Roewer to be preoccupied by *Aranea dorsalis* Fabricius, 1775.
Aranea elegantula Roewer, 1942: 841, new name for *Epeira elegans* Blackwall, 1862, erroneously thought to be preoccupied by *Aranea elegans* Meyer, 1790.
Aranea minutella Roewer, 1942: 847, new name for *Epeira minuta* Nicolet, 1849, erroneously thought by Roewer to be preoccupied by *Aranea minuta* Meyer, 1790.
Aranea mundatula Roewer, 1942: 847, new name for *Epeira munda* Blackwall, 1863, preoccupied by *Epeira munda* C. L. Koch, 1836.
Aranea perfoliatus Franganillo Balboa, 1930.
Aranea quadrimaculosa Roewer, 1942: 850, new name for *Epeira quadrimaculata* Nicolet, 1849: 507, erroneously thought by Roewer to be preoccupied by *Aranea quadrimaculata* De Geer, 1778.
Aranea quadripunctatula Roewer, 1942: 850, new name for *Epeira quadripunctata* Nicolet, 1849, erroneously thought by Roewer to be preoccupied by *Aranea quadripunctata* Linn., 1758.
Aranea rapaxata Roewer, 1942: 850, new name for *Epeira rapax* Blackwall, 1863, erroneously thought by Roewer to be preoccupied by *Aranea rapax* Fabricius, 1798.
Araneus advena Petrunkevitch, 1911: 277, new name for *Epeira adianta* Nicolet, 1849: 488, preoccupied by *Epeira adianta* Walckenaer, 1802.
Araneus aequiangulus ochraceus Franganillo Balboa, 1936: 70.
Araneus anuncinatus depilosus Franganillo Balboa, 1930: 29.
Araneus balboae Brignoli, 1983: 262, new name for *Aranea conicus* Franganillo Balboa, 1946, preoccupied by *Aranea conica* Pallas, 1772.
Araneus bormensis Berland, 1913: 94, pl. 9, figs. 46, 47, ♀.
Araneus bourguyi Mello-Leitão, 1915: 135.
Araneus conicus Franganillo Balboa, 1946: 97, figs. 1, 2, ♀.
Araneus consimilis Mello-Leitão, 1915: 133.
Araneus contestationis di Caporiacco, 1954: 105, fig. 25, ♀. Type lost (not in MNHN, MZUF).
Araneus franganillianus Brignoli, 1983: 262, new name for *Araneus niger* Franganillo Balboa, 1936, preoccupied by *Araneus niger* Lister, 1778.
Araneus franganilloides Brignoli, 1983: 262, new name for *Araneus rugosus* Franganillo Balboa, 1936: 75, preoccupied by *Araneus rugosus* Badcock, 1932.
Araneus intrepida Mello-Leitão, 1915: 104.
Araneus itatiayae Mello-Leitão, 1915: 133.
Araneus nephiloides trapezoidalis Franganillo Balboa, 1930.
Araneus niger Franganillo Balboa, 1936: 73.
Araneus nigrocellatus di Caporiacco, 1954: 110, fig. 28. Type lost (not in MNHN, MZUF).
Araneus petri Simon, 1897: 6. Holotype at University of Torino destroyed in Second World War.
Araneus rugosus Franganillo Balboa, 1936: 75, fig. 33, ♀.
Araneus sulphureus Franganillo Balboa, 1930: 29.
Epeira adianta Nicolet, 1849: 483.
Epeira affinis Nicolet, 1849: 498, preoccupied by Blackwall, 1846.
Epeira astuta Blackwall, 1863: 36.
Epeira bicaudata Nicolet, 1849: 510.
Epeira carenata Nicolet, 1849: 509.
Epeira cauta Walckenaer, 1841: 35.
Epeira cruciata Nicolet, 1849: 494, preoccupied by Walckenaer, 1805.
Epeira decaspina Taczanowski, 1873: 143. Holotype lost in PAN.
Epeira depressa Walckenaer, 1841: 134.
Epeira dorsalis Nicolet, 1849: 499.
Epeira elegans Blackwall, 1862: 431.
Epeira flavifrons Nicolet, 1849: 507.
Epeira foliplicans Hingston, 1932: 367.
Epeira folisecens Hingston, 1932: 364.
Epeira fuliginosa Walckenaer, 1841: 41.
Epeira fumida Blackwall, 1862: 433.
Epeira grammica Blackwall, 1862: 434.
Epeira immunda Nicolet, 1849: 510.
Epeira lepida Blackwall, 1862: 430.
Epeira lodiculafaciens Hingston, 1932: 365.
Epeira luteola Blackwall, 1862: 435.
Epeira magellanica Walckenaer, 1847: 467.
Epeira minuta Nicolet, 1849: 508.
Epeira moraballii Hingston, 1932: 363.
Epeira mucronata Blackwall, 1862: 438.
Epeira multiguttata Blackwall, 1862: 432.
Epeira munda Blackwall, 1863: 33.
Epeira naevia Nicolet, 1849: 499.
Epeira nidificans Hingston, 1932: 367.
Epeira obliterata Nicolet, 1849: 496.
Epeira perplexa Walckenaer, 1841: 101.
Epeira prostypa Walckenaer, 1841: 136.
Epeira quadrimaculata Nicolet, 1849: 507.
Epeira quadripunctata Nicolet, 1849: 495.
Epeira rapax Blackwall, 1863: 22.
Epeira sacculifaciens Hingston, 1932: 364.
Epeira scitula Blackwall, 1863: 37.
Epeira spira Walckenaer, 1841: 80.
Epeira transversalis Nicolet, 1849: 493.
Epeira valdiviensis Nicolet, 1849: 506.
Epeira viridipes Taczanowski, 1878: 155.

Keys for *Araneus* species

The keys presented here do not include the three species *A. andrewsi*, *A. gemmoides*, and *A. montereyensis*, with distributions mainly north of Mexico, but some records in Baja California Norte.

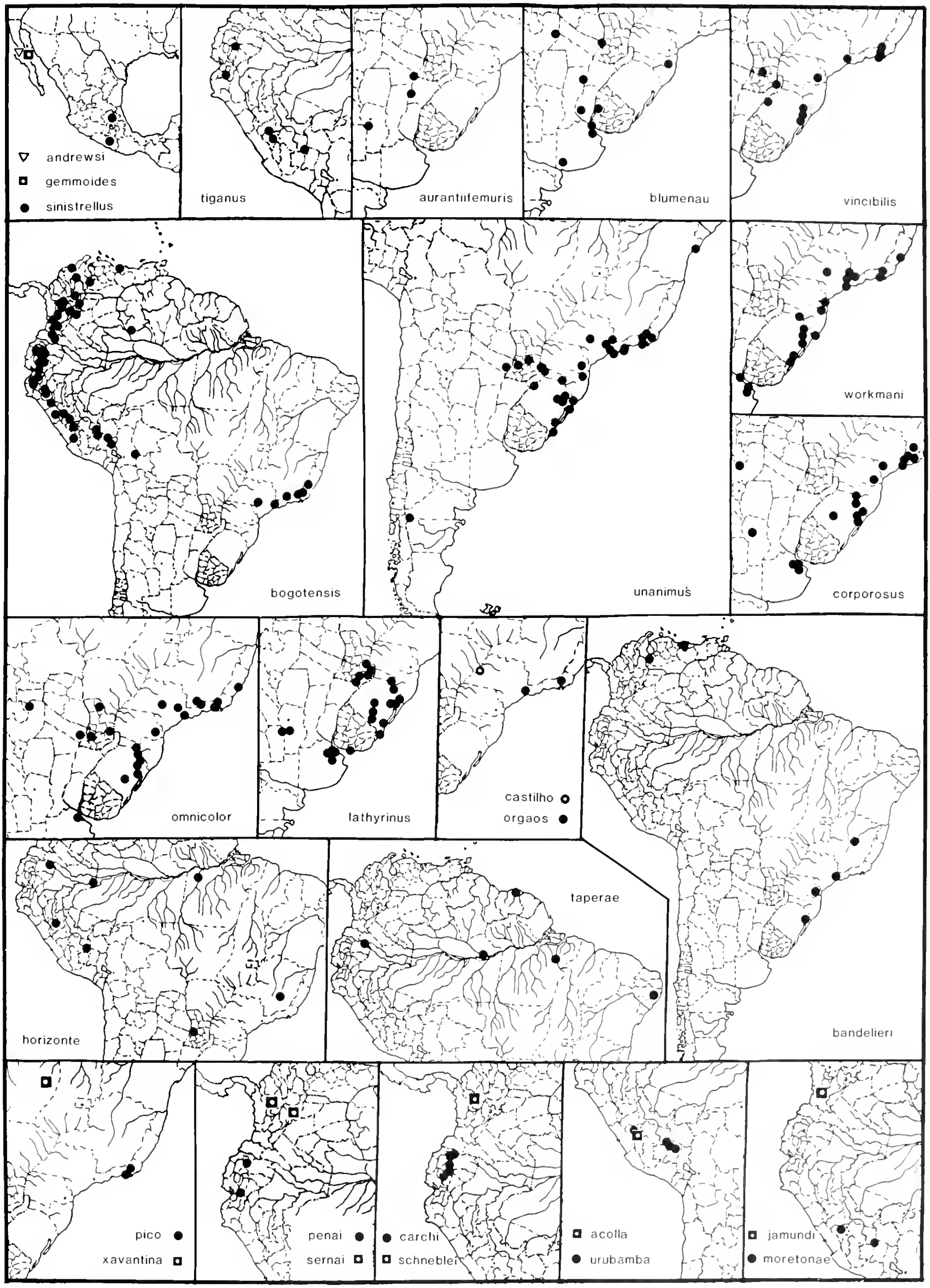
There were problems in making keys. The females of some species have the scape torn off the diagnostic epigynum when mating. Thus they may be collected with or without scape (usually without), but in-

dividuals with the scape are not found in the available collections.

Males have a diagnostically shaped embolus in the palpus. The embolus is partly or completely hidden by the conductor and other structures. Also the embolus may or may not have an embolus cap. Unless many specimens are available, we do not know whether the cap is present or not. The prominent median apophysis is variable in shape in many species.

Key to Female *Araneus* from Mexico and the Neotropics

1 Scape torn off in mated individuals (Figs. 10, 326, 330, 511, 515) ... 2
– Epigynum with a scape ... 10
2(1). Lateral plates of epigynum triangular in posterior view (Figs. 322, 327) ... 3
– Lateral plates otherwise ... 4
3(2). A pair of seminal receptacles visible through transparent exoskeleton anterior of a semicircular ridge (Fig. 326); São Paulo, Brazil (Map 3) ... *lenkoi*
– Seminal receptacles not visible anterior of circular ridge (Fig. 321); Rio de Janeiro State to Paraná, Brazil (Map 3) ... *iguacu*
4(2). Median plate small and pentagonal in posterior view (Fig. 331); Colombia (Map 3) ... *chingaza*
– Median plate otherwise ... 5
5(4). Median plate projecting ventrally beyond lateral plates (Fig. 11); lateral plates each with a sclerotized ventral thumb (Fig. 11); Ecuador, Peru (Map 2) ... *tiganus*
– Median plate otherwise ... 6
6(5). Lateral plate in shape of thin wings in posterior view (Fig. 407); Mexico, Central America (Map 5) ... *flavus*
– Lateral plates otherwise ... 7
7(6). Openings less than their diameter apart (Fig. 499); Oaxaca, Mexico (Map 5) ... *ocaxa*
– Openings more than 1.5 diameters apart (Figs. 376, 511, 515); Mexico ... 8
8(7). Openings facing median (Fig. 515); central Mexico (Map 5) ... *tellezi*
– Opening facing laterally (Figs. 376, 511), central Mexico (Map 5) ... 9
9(8). Openings on lateral edge (Fig. 376); Pacific Coast, Mexico (Map 5) ... *colima*
– Openings some distance from edge (Fig. 511), central Mexico (Map 5) ... *tenancingo*
10(1). Scape of epigynum as long as 1.5 times its width; or scape without wrinkles (Figs. 9, 404, 410) ... 11
– Scape at least twice as long as wide and with transverse wrinkles ... 25
11(10). Scape oval and with anterior notch (Fig. 9); Ecuador, Peru (Map 2) ... *tiganus*
– Scape otherwise ... 12
12(11). Abdomen oval, longer than wide with longitudinal bands (Figs. 408, 412) ... 13
– Abdomen otherwise ... 14
13(12). Scape with a stalk (Fig. 404); Mexico to Nicaragua (Map 5) ... *flavus*
– Scape broadly attached (Fig. 410); Pacific Coast, Mexico (Map 5) ... *tepic*
14(12). Abdomen wider than long with lateral points (Fig. 341); Central America to Amazon (Map 5) ... *sextus*
– Abdomen otherwise ... 15
15(14). Hispaniola (Map 5) ... 16
– Continental ... 17
16(15). Spotted legs ... *hispaniola*
– Uniform orange legs ... *bryantae*
17(15). Scape wider than area of base visible on either side (Figs. 5, 211, 376) ... 18
– Area of base visible on either side wider than diameter of scape (Fig. 343); Costa Rica (Map 5) ... *microsoma*
18(17). Scape triangular (Figs. 5, 211) ... 19
– Scape circular (Fig. 376) ... 20
19(18). Epigynum in posterior view with triangular depression (Fig. 6); more than 10 mm total length; Mexico (Map 2) ... *sinistrellus*
– Epigynum with large median plate in posterior view (Fig. 212); less than 9 mm total length; Guatemala (Map 5) ... *guatemus*
20(18). Epigynum with a bordered opening in ventral view (Figs. 369, 376, 381) ... 21
– Epigynum otherwise (Figs. 215, 372, 400) ... 23
21(20). Scape stalked (Fig. 376); abdomen oval (Fig. 378); Pacific Coast, Mexico (Map 5) ... *colima*
– Scape broadly attached (Figs. 369, 381); abdomen widest anteriorly (Figs. 371, 383) ... 22
22(21). Openings close to scape (Fig. 381); Guerrero, Mexico (Map 5) ... *lanio*
– Openings some distance from scape (Fig. 369); Cuba (Map 5) ... *faxoni*
23(20). Slits posteriorly on base on each side of scape in ventral view (Fig. 400); Pacific Coast, Mexico (Map 5) ... *mazamitla*
– Epigynum otherwise (Figs. 215, 372) ... 24
24(23). Median plate in posterior view with ventral notch (Fig. 373); width of



Map 2. Distribution of *Araneus* species.

area of base visible on each side of scape less than half diameter of scape (Fig. 372); Bahamas (Map 5) ... *bimini*

– Median plate in posterior view without ventral notch (Fig. 216); width of area of base visible on each side of scape more than half diameter of scape (Fig. 215); Guatemala (Map 3) ... *rufipes*

25(10). Scape twisted sideways on itself (Figs. 122, 312, 457) ... 26

– Scape straight or twisted anteriorly on itself (Figs. 1, 17, 37, 58, 290) ... 41

26(25). Mexico, Guatemala ... 29

– Costa Rica, Panama, South America ... 27

27(26). Posterior median plate wrinkled (Fig. 123); wrinkles visible on posterior edge in ventral view (Fig. 122); Ecuador (Map 2) ... *carchi*

– Posterior median plate smooth (Figs. 296, 309); posterior edge in ventral view smooth (Figs. 295, 303) ... 28

28(27). Epigynum in posterior view with two circular depressions on anterior edge of median plate (Figs. 304, 309, 313); Central America to northern Argentina (Map 4) ... *guttatus*

– Epigynum in posterior view lacking circular depressions (Figs. 296, 301); Panama to Paraguay (Map 4) ... *venatrix*

29(26). Scape with two or more sideways twists on itself (Figs. 457, 462) ... 35

– Scape with only one sideways twist on itself (Figs. 445, 466, 507) ... 30

30(29). Base with a sphere on each side of scape (Figs. 445, 482) ... 31

– Base otherwise ... 32

31(30). Spheres of base sclerotized (Fig. 445); with two slits in ventral view (Fig. 446); Texas, Arizona, northern Mexico (Map 5) ... *cochise*

– Spheres of base not sclerotized (Fig. 482); with two round depressions in posterior view (Fig. 483); central Mexico (Map 5) ... *puebla*

32(30). Median plate rectangular, anteriorly fused (Fig. 471); a round depression on each side in ventral view (Fig. 470); central Mexico (Map 5) ... *quirapan*

– Median plate wider ventrally than dorsally (Figs. 467, 478, 508) ... 33

33(32). Seminal receptacle showing as a dark spot on each side of scape (Fig. 507); New Mexico, Arizona to northern Mexico (Map 5) ... *arizonensis*

– Base of epigynum otherwise (Figs. 466, 477); central Mexico ... 34

34(33). Base of epigynum with a depression on each side of scape having a lip on the median side (Fig. 466); (Map 5) ... *popago*

– No such depression and lip present (Fig. 477); (Map 5) ... *mendoza*

35(29). Posterior edge with a nipple on each side of scape (Fig. 474); Guerrero, Mexico (Map 5) ... *nacional*

– Posterior edge otherwise (Figs. 462, 503) ... 36

36(35). Openings visible on posterior (Fig. 504); Chiapas, Mexico (Map 5) ... *baul*

– Openings visible on venter (Figs. 470, 487, 494) ... 37

37(36). Posterior edge in ventral view concave (Fig. 494); Michoacan, Mexico (Map 5) ... *anguinifer*

– Posterior edge in ventral view with median projection (Figs. 462, 470) ... 38

38(37). A diagonal slit visible on each side of scape (Fig. 487); Arizona to central Mexico (Map 5) ... *guerrerensis*

– Epigynum otherwise (Figs. 457, 462, 470) ... 39

39(38). A circular ridge on each side of scape in ventral view (Fig. 457); central Mexico (Map 5) ... *leones*

– Epigynum without circular ridge (Figs. 462, 470) ... 40

40(39). Median plate in posterior view ventrally fused to laterals (Fig. 471); central Mexico (Map 5) ... *quirapan*

– Median plate heart-shaped (Fig. 463); Mexico (Map 5) ... *salto*

41(25). Chile, and Argentine Andes ... 42

– Neotropics outside of Chile and of Argentine Andes ... 47

42(41). Epigynum in posterior view longer than wide with a pair of circular depressions (Fig. 268); (Map 3) ... *titirus*

– Epigynum otherwise ... 43

43(42). Base of epigynum in ventral view with a transverse lobe on each side (Fig. 258); (Map 3) ... *huahun*

– Epigynum otherwise ... 44

44(43). Base of epigynum subtriangular in ventral view with sclerotized, dark lateral plates visible on each side (Fig. 245); (Map 3) ... *talca*

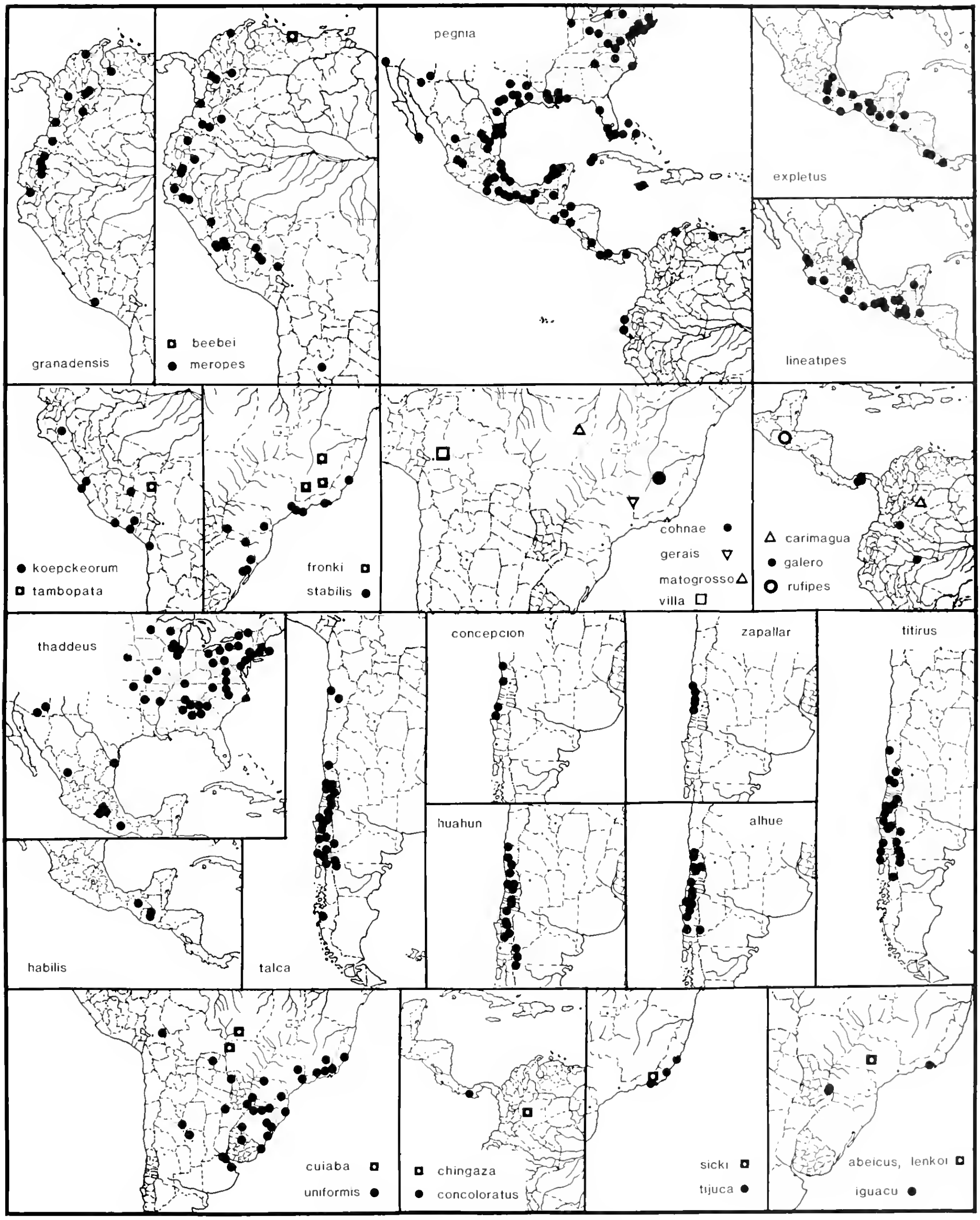
– Epigynum otherwise ... 45

45(44). Median plate in posterior view with a V-shaped depression (Figs. 251, 255) ... 46

– Median plate with semicircular wrinkles (Fig. 263); (Map 3) ... *alhue*

46(45). V-shaped depression forming an acute angle dorsally (Fig. 251); (Map 3) ... *concepcion*

– V-shaped depression forming a right



Map 3. Distribution of *Araneus* species.

angle dorsally (Fig. 255); (Map 3) .... *zapallar*

47(41). Greater Antilles 48

– Continental and Trinidad 50

48(47). Base of epigynum with a round depression on each side of scape (Figs. 357, 361); Hispaniola 49

– Base with a slit on each side of scape

(Fig. 414), Puerto Rico (Map 5) *adjuntaensis*

49(48). Ventral depression with an anterior lip only (Fig. 357); Hispaniola (Map 5) *elizabethae*

– Ventral depression with anterior and posterior lips (Fig. 361); Hispaniola (Map 5) *hotteiensis*

50(47). Median and lateral plates in posterior view fused and projecting ventrally on each side (Fig. 396); scape gradually widening distally (Fig. 395); southern U.S. to Colombia (Map 5) *detrimentosus*

– Epigynum otherwise ... 51

51(50). Base with a V-shaped slit opening ventrally on each side of scape with dark seminal receptacles showing at posterior end of slit (Fig. 228); abdomen oval, wider than long, with a transverse white patch on venter (Figs. 232, 233); eastern and southern U.S. to Colombia and Ecuador (Map 3) *pegnia*

– Base of epigynum otherwise ... 52

52(51). Length of scape about two to three times its width (Fig. 435) ... 53

– Length of scape more than four times its width (Fig. 1) ... 66

53(52). South America ... 54

– Mexico, Central America ... 58

54(53). Median plate triangular, ventrally bulging (Fig. 110); Colombia (Map 2) ... *sernai*

– Median plate otherwise ... 55

55(54). Median plate narrow with parallel sides (Fig. 348); Peru (Map 5) ... *lintatus*

– Median plate otherwise ... 56

56(55). Openings in lateral plates on venter (Figs. 146, 147); Colombia to Peru (Map 3) *granadensis*

– Openings otherwise ... 57

57(56). In ventral view, median plate bulging on each side of scape (Fig. 138); Peru (Map 2) ... *acolla*

– In ventral view, median plate bulging as a transverse swelling behind posterior margin of base (Fig. 117); Rio de Janeiro State, Brazil (Map 2) *pico*

58(53). A spherical bulge on each side of scape (Fig. 445); southern U.S. to northern Mexico (Map 5) *cochise*

– Scape otherwise 59

59(58). Base in ventral view with transverse groove (Fig. 389); Costa Rica (Map 5) *ana*

– Epigynum otherwise 60

60(59). A loop of duct visible on base on each side of scape (Fig. 122); Costa Rica (Map 5) *ubicki*

– Epigynum otherwise 61

61(60). A dark sphere visible through base on each side of scape (Fig. 418); Guerrero, Mexico (Map 5) ... *caballo*

– Epigynum otherwise ... 62

62(61). Base with openings on each side of scape facing laterally (Fig. 435); Chiapas, Mexico (Map 5) ... *cristobal*

– Epigynum otherwise ... 63

63(62). In posterior view, a pair of oval lateral plates almost touching (Fig. 336); Guatemala, Costa Rica (Map 5) ... *selva*

– Epigynum otherwise ... 64

64(63). Scape wider than part of base visible on each side in ventral view (Fig. 449); central Mexico (Map 5) ... *dreisbachi*

– Part of base on each side of scape as wide as or wider than scape (Figs. 440, 453) ... 65

65(64). Base with an edge on each side of scape, parallel with scape (Fig. 453); central Mexico (Map 5) ... *desierto*

– Base entire (Fig. 440); Guerrero, Mexico (Map 5) ... *axacus*

66(52). Scape projecting from posterior margin of base (Fig. 153); Peru (Map 3) ... *tambopata*

– Epigynum otherwise ... 67

67(66). Epigynum with large round bordered opening in ventral or posterior view (Figs. 100, 102, 113) ... 68

– Epigynum otherwise ... 69

68(67). Openings ventral on each side of scape (Fig. 113) ... 70

– Openings posterior on each side (Figs. 100, 102); Amazon (Map 2) ... *horizonte*

69(67). Openings to side of scape (Fig. 113); median plate narrowing ventrally in posterior view (Fig. 114); Venezuela, Brazil (Map 2) ... *bandelieri*

– Opening lateral on base (Fig. 168); median plate wide in posterior view (Fig. 169); Peru to northern Chile (Map 3) ... *koepckeorum*

70(68). Length of scape about twice that of base (Figs. 272, 276, 279) ... 71

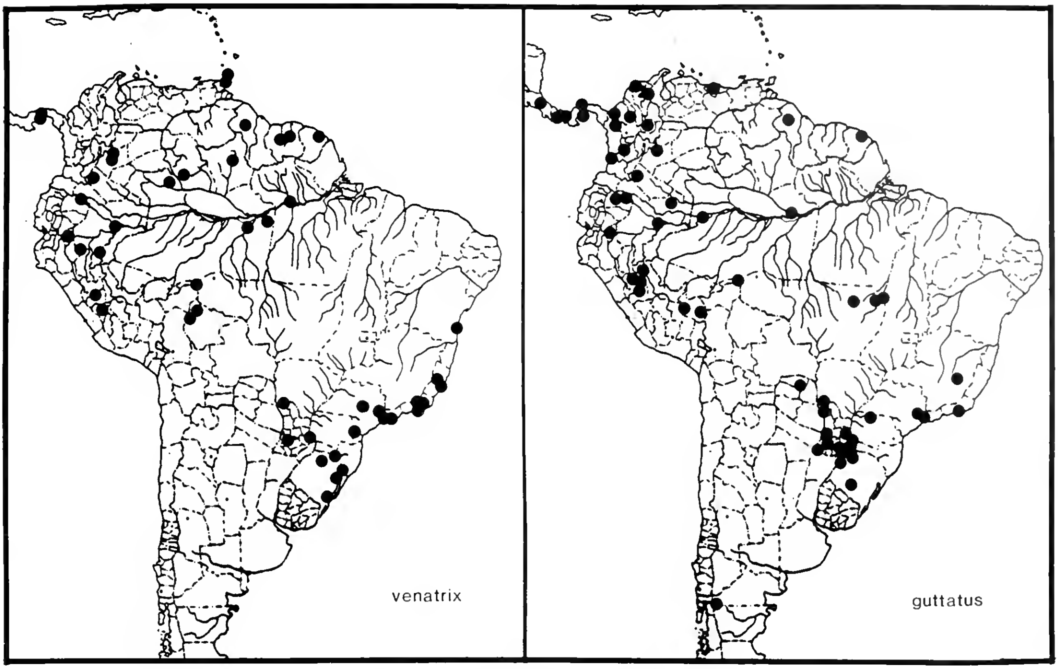
– Scape only slightly extending beyond base (Figs. 24, 282) ... 73

71(70). Base in ventral view entire (Fig. 279); median plate in posterior view anteriorly fused (Fig. 280); Bolivia (Map 3) ... *villa*

– Base with lobes on each side of scape (Figs. 272, 276); median plate triangular (Figs. 273, 277) ... 72

72(71). Median plate longer than wide (Fig. 273); Bolivia, Brazil, Argentina (Map 3) ... *uniformis*

– Median plate wider than long (Fig. 277); Mato Grosso, Brazil (Map 3) ... *cuiaba*



Map 4. Distribution of *Araneus* species.

73(70). Scape distally pointed (Fig. 290); median plate bulging posteriorly behind transverse edge of base (Fig. 290); Espírito Santo, Rio de Janeiro States, Brazil (Map 3) .... *tijuca*

– Scape usually distally rounded, base otherwise 74

74(73). Abdomen with lateral humps (Figs. 318, 387) 75

– Abdomen without humps 76

75(74). Scape of epigynum distally expanded (Fig. 386); Pacific Coast, Mexico (Map 5) .... *boneti*

– Scape of epigynum distally narrowed (Fig. 316); São Paulo State, Brazil (Map 3) .... *abeicus*

76(74). Mexico, Central America 77

– South America 82

77(76). Venter of first femur with black longitudinal lines (Fig. 242); Mexico to Honduras (Map 3) .... *lineatipes*

– Venter of femur never with longitudinal lines 78

78(77). A longitudinal rectangular depression on each side of scape (Fig. 223); venter of abdomen with black square (Fig. 226); Panama, Colombia (Map 3) .... *galero*

– Epigynum otherwise; venter of abdomen otherwise 79

79(78). Venter of epigynum with transverse sculpturing (Figs. 219, 235) 80

– Venter of epigynum with longitudinal or diagonal sculpturing (Figs. 193, 197, 282) 81

80(79). A concave edge on each side of scape (Fig. 235); median plate large and rectangular, wider than long in posterior view (Fig. 236); eastern U.S., Arizona to Guerrero, Mexico (Map 3) .... *thaddeus*

– A transverse slit on each side of scape with lateral plates overhanging median plate on sides (Fig. 219); posterior view as in Figure 220; Chiapas, Guatemala (Map 3) .... *habilis*

81(79). A diagonal dark mark on each side of scape (Fig. 282); posterior median plate triangular (Fig. 283); Panama (Map 3) .... *concoloratus*

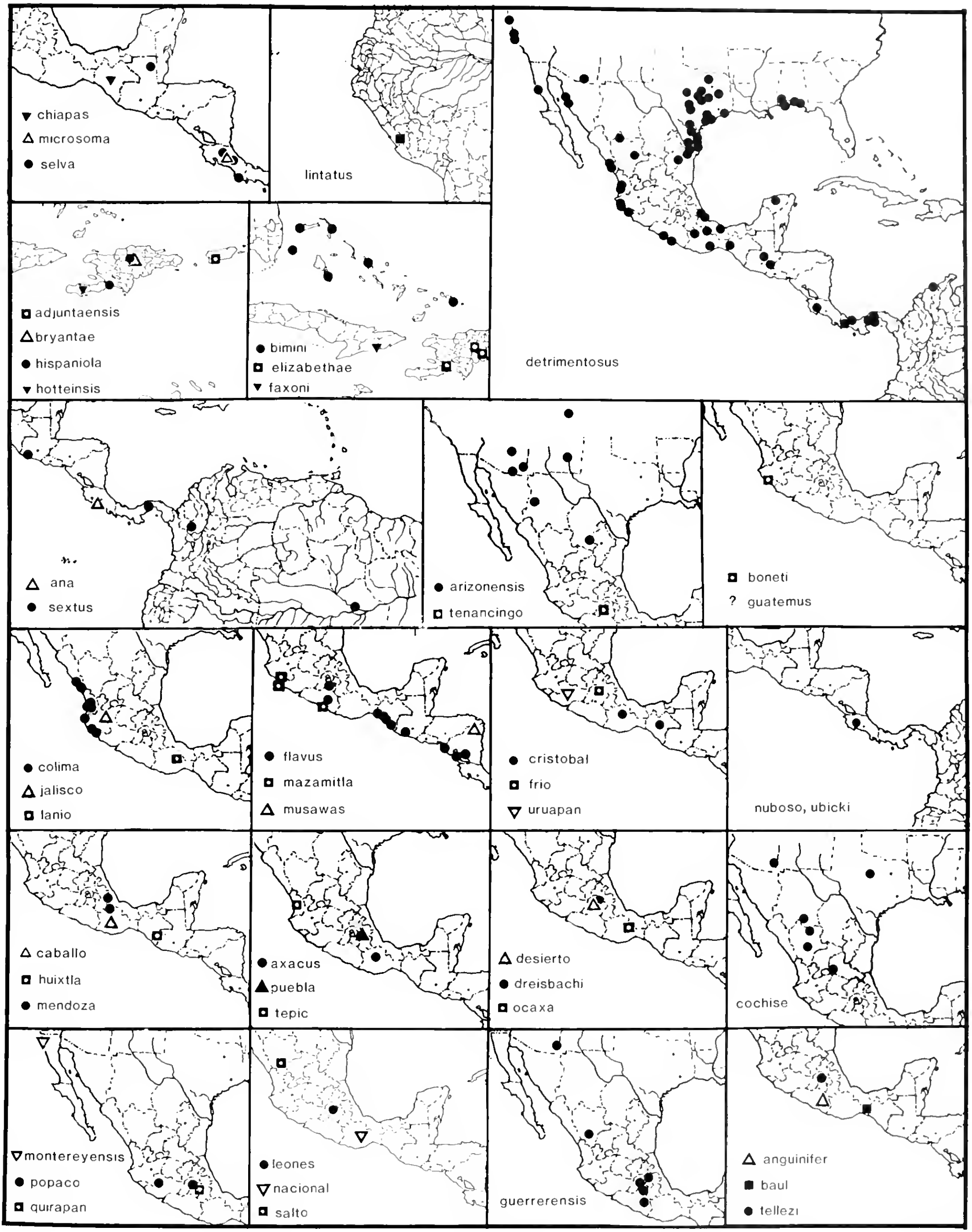
– Epigynum without diagonal mark in ventral view (Figs. 193, 197, 199); posterior plate rounded (Figs. 194, 198, 200); central Mexico to Panama (Map 3) .... *expletus*

82(76). Epigynum with a wrinkled structure below scape (Fig. 286); Rio de Janeiro State, Brazil (Map 3) .... *sicki*

– Epigynum otherwise 83

83(82). Posterior margins in ventral view lobed

(Figs. 128, 133); posterior median plate barely framed by narrow lateral plates with transverse grooves (Figs. 129, 134); Ecuadorian, Peruvian Andes ... 84
– Epigynum otherwise ... 85
84(83). In posterior view lateral plates surround median plate ventrally (Fig. 134); (Map 2) ... *urubamba*
– In posterior view lateral plates surround median plate only on sides and posterior (Fig. 129); Ecuadorian Andes (Map 2) ... *penai*
85(83). Median plate in posterior view twice as long as wide and lateral plates narrow, about four times as long as wide (Fig. 175); southern Brazil (Map 3) ... *stabilis*
– Epigynum otherwise ... 86
86(85). A depression at ventral end of lateral plates, seen in ventral and posterior views (Figs. 146, 147); scape wide and with sides parallel (Fig. 146) and posterior median plate rectangular, longer than wide (Fig. 147); Colombia to Peru (Map 3) ... *granadensis*
– Epigynum otherwise ... 87
87(86). A finger from lateral plate "overhanging" median plate in posterior view as in Figures 2, 33; scape looping anteriorly (Figs. 1, 17, 32); Colombia to Brazil (Map 2) ... *bogotensis*
– Epigynum otherwise ... 88
88(87). Median plate in posterior view distinctly narrower than lateral plates and median plate only slightly wider dorsally than ventrally (Figs. 180, 185); median plate in ventral view forms a bulge (Figs. 179, 184) ... 89
– Epigynum otherwise ... 90
89(88). Median plate wrinkled (Fig. 185), wider than lateral plates in ventral view (Fig. 184); Venezuela (Map 3) ... *beebei*
– Median plate smooth (Fig. 180) narrower than lateral plates in ventral view (Fig. 179); Minas Gerais, Brazil (Map 3) ... *fronki*
90(88). In posterior view lateral plates twisted (Figs. 161, 163); Colombia to Bolivia (Map 3) ... *meropes*
– Lateral plates never twisted in posterior view ... 91
91(90). Median plate a stalked square (Figs. 25, 38) ... 92
– Median plate otherwise ... 93
92(91). Scape looping anteriorly (Fig. 24); abdomen dark in color; Colombia to Brazil (Map 2) ... *bogotensis*
– Scape without anterior loop (Fig. 37); abdomen light with tiny silver platelets (Fig. 39); Bolivia, Argentina (Map 2) ... *aurantiifemuris*
93(91). Median plate in posterior view with constriction ventrally (Figs. 72, 79); in ventral view a median lobe and a pair of lateral lobes overhung by anterior of base (Figs. 71, 78) ... 94
– Epigynum otherwise ... 95
94(93). Median plate wider than lateral plates (Fig. 72); southern Brazil, Argentina (Map 2) ... *corporosus*
– Median plate as wide as or narrower than lateral plates (Fig. 79); southern Brazil, Argentina (Map 2) ... *workmani*
95(93). Median plate in posterior view a stalked pentagonal, widest in middle (Figs. 59, 106) ... 96
– Median plate never pentagonal (Figs. 50, 65) ... 97
96(95). In ventral view a median constriction of raised area under scape (Fig. 105); Amazon, eastern Brazil (Map 2) ... *taperae*
– In ventral view, a longitudinal slit on each side of scape (Fig. 58); Brazil, Paraguay, Argentina (Map 2) ... *unanimus*
97(95). Base of epigynum in ventral view with posterior diagonal slit (Figs. 85, 92, 95) ... 98
– Epigynum otherwise (Figs. 49, 64, 142) ... 100
98(97). Median plate in posterior view with a pair of distinct ventral dimples (Fig. 86); lateral plates with distinct ventral median angles (Fig. 86); southern Brazil, Paraguay, Argentina (Map 2) ... *lathyrinus*
– Median plate without dimples; lateral plates rounded (Figs. 93, 96) ... 99
99(98). Lateral plates widest dorsally; median edge of lateral plates in posterior view with a curl ventrally (Fig. 96); Colombia (Map 2) ... *schneblei*
– Lateral plates with sides about parallel; median edge of lateral plates in posterior view turning to sides (Fig. 93); Rio de Janeiro, São Paulo States, Brazil (Map 2) ... *orgaos*
100(97). Median plate oval, with curved transverse grooves dorsally (Fig. 50); southern Brazil, Paraguay, northern Argentina (Map 2) ... *omnicolor*
– Median plate otherwise (Figs. 43, 65, 143) ... 101
101(100). Median plate ventrally projecting beyond lateral plates (Fig. 43); lateral plates with pointed ventral tip (Fig. 43); southern Brazil, Argentina (Map



Map 5. Distribution of *Araneus* species.

2 ... *blumenau*
– Epigynum otherwise ... 102
102(101). Lateral plates with median ventral angle (Fig. 143); Peru (Map 2) ... *moretonae*
– Lateral plates with rounded median edge (Fig. 65); southern Brazil, Paraguay (Map 2) ... *vincibilis*

Key to Male *Araneus* from Mexico and the Neotropics

1 First coxa with hook on distal margin ... 39
– First coxa without hook ... 2
2(1). Median apophysis of palpus with one proximal spine and a distal "fish-tail" end (Fig. 431) or distal frayed end, or distal numerous teeth (Figs. 342, 519) ... 3
– Median apophysis otherwise (sometimes with minute distal knob or teeth in palpi with embolus making counterclockwise turn in left palpus) ... 16
3(2). Spine in middle of median apophysis pointing toward base of cymbium (Fig. 342); Guatemala to Amazon (Map 5) ... *sextus*
– Spines pointing toward middle or distal end of cymbium (Figs. 481, 486) ... 4
4(3). Embolus visible and coiled clockwise in left palpus (Figs. 481, 486, 497) ... 5
– Embolus coiled counterclockwise straight or hidden ... 11
5(4). Embolus only slightly curved or tightly coiled (Figs. 426, 493, 519) ... 6
– Embolus with a grand loop through distal portion of bulb (Figs. 481, 486, 497) ... 8
6(5). Embolus without distal coil (Fig. 426); Costa Rica (Map 5) ... *ubicki*
– Embolus with distal coil (Figs. 493, 519) ... 7
7(6). Conductor with a distal lobe in mesal view of palpus (Fig. 493); Arizona to central Mexico (Map 5) ... *guerrerensis*
– Conductor distally pointed (Fig. 519); central Mexico (Map 5) ... *tellezi*
8(5). Embolus with curved filamentous portion originating in a base (Figs. 481, 486, 502) ... 9
– Embolus without set-off base as in Figure 497; Chiapas, Mexico (Map 5) ... *huixtla*
9(8). Base of embolus expanded (Fig. 481); central Mexico ... *mendoza*
– Base of embolus otherwise (Figs. 486, 502) ... 10
10(9). Filamentous portion of embolus originating distally from base (Fig. 486); central Mexico (Map 5) ... *puebla*
– Filamentous portion originating proximally from base (Fig. 502); Oaxaca, Mexico (Map 5) ... *ocaxa*
11(4). Embolus a slightly curved rod (Fig. 456); central Mexico (Map 5) ... *desierto*
– Embolus otherwise ... 12
12(11). Embolus a counterclockwise filament in left palpus (Fig. 439); Chiapas, Mexico (Map 5) ... *cristobal*
– Embolus otherwise ... 13
13(12). Width of conductor in mesal view almost twice its length (Fig. 452); central Mexico (Map 5) ... *dreisbachi*
– Conductor in mesal view about as wide as long (Figs. 431, 461, 469) ... 14
14(13). Terminal apophysis "hanging down" and pointed (Fig. 431); Costa Rica (Map 5) ... *nuboso*
– Terminal apophysis otherwise; central Mexico ... 15
15(14). Terminal apophysis with rounded bulge as in Figure 469; (Map 5) ... *popaco*
– Terminal apophysis otherwise, as in Figure 461; (Map 5) ... *leones*
16(2). Median apophysis with one spine (Figs. 375, 388) ... 17
– Median apophysis with two or more spines or knobs (Figs. 190, 346, 351) ... 31
17(16). Embolus coiled clockwise in left palpus (Figs. 426, 448) ... 18
– Embolus otherwise ... 19
18(17). Embolus gently curved as in Figure 426; Costa Rica (Map 5) ... *ubicki*
– Embolus with a large loop as in Figure 448; Texas, Arizona to central Mexico (Map 5) ... *cochise*
19(17). Embolus curved counterclockwise in left palpus (Figs. 392, 439, 444) ... 20
– Embolus not visible or otherwise ... 25
20(19). Embolus originating from "top" of bulb (Figs. 403, 409, 427) ... 22
– Embolus U-shaped and originating from center of bulb (Figs. 392, 444) ... 21
21(20). Terminal apophysis distally narrow (Fig. 392); central Mexico (Map 5) ... *jalisco*
– Terminal apophysis triangular (Fig. 444); Guerrero, Mexico (Map 5) ... *axacus*
22(20). Conductor very wide, almost touching cymbium (Fig. 427); Nicaragua (Map 5) ... *musawas*
– Conductor otherwise ... 23
23(22). Spine of median apophysis pointed toward distal end of palpus, embolus loop small as in Figure 439; Chiapas, Mexico (Map 5) ... *cristobal*
– Median apophysis otherwise (Figs. 403, 409) ... 24
24(23). Terminal embolus loop distal of embolus base in bulb as in Figure 409; central Mexico to Nicaragua (Map 5) ... *flavus*
– Terminal embolus loop proximal of em-

bolus base in bulb as in Figure 403; central Mexico (Map 5) .... *mazamitla*
25(19). Tip of embolus overhanging conductor (Figs. 380, 433) 26
– Embolus otherwise 27
26(25). Median apophysis almost rectangular (Fig. 380); Pacific Coast, Mexico (Map 5) .... *colima*
– Median apophysis round (Fig. 433); central Mexico (Map 5) .... *uruapan*
27(25). Conductor in mesal view of palpus much higher than wide (Fig. 452); central Mexico (Map 5) .... *dreisbachi*
– Conductor otherwise (Figs. 375, 429, 469) 28
28(27). Conductor stalked and much smaller than median apophysis (Fig. 429); central Mexico (Map 5) .... *frio*
– Conductor otherwise (Figs. 375, 388, 469) 29
29(28). Median apophysis round with spine on its side (Fig. 375); Bahamas (Map 5) .... *bimini*
– Median apophysis otherwise (Figs. 388, 469) 30
30(29). Terminal apophysis narrow and pointed distally (Fig. 388); Mexico (Map 5) .... *boneti*
– Terminal apophysis a bulging lobe (Fig. 469); central Mexico (Map 5) .... *popaco*
31(16). Median apophysis with two spines or lobes (Figs. 346, 351, 514) 32
– Median apophysis usually with three spines (Figs. 183, 191, 227, 510) 34
32(31). Median apophysis with two round knobs (Fig. 351); Chiapas, Mexico (Map 5) .... *chiapas*
– Median apophysis otherwise 33
33(32). Median apophysis with two lateral hooks (Fig. 346); Costa Rica (Map 5) .... *microsoma*
– Median apophysis with two large spines pointing toward distal end of cymbium (Fig. 514); central Mexico (Map 5) .... *tenancingo*
34(31). Median apophysis with one large and two smaller spines (Fig. 510); New Mexico, Arizona, northern Mexico (Map 5) .... *arizonensis*
– Median apophysis with two larger and one smaller, or one blunt spine (Figs. 189–191, 227) 35
35(34). Median apophysis as in Figure 227; Central America, Colombia (Map 3) .... *galero*
– Median apophysis otherwise; South America 36
36(35). Palpal patella with only one seta; embolus a straight prong (Fig. 188); Minas Gerais, Brazil (Map 3) .... *cohnae*
– Palpal patella with two setae; embolus a twisted structure (Figs. 189–191) 37
37(36). Median apophysis longer than wide (Fig. 189); Mato Grosso, Brazil (Map 3) .... *matogrosso*
– Median apophysis as wide as long (Figs. 190, 191) 38
38(37). Distal spine of median apophysis small (Fig. 190); Colombia (Map 3) .... *carimagua*
– Distal spine of median apophysis wide, blunt (Fig. 191); Minas Gerais, Brazil (Map 3) .... *gerais*
39(1). Proximal end of elongate median apophysis with a pair of spines (Figs. 157, 299, 325) 50
– Proximal end of median apophysis with one spine (Fig. 399) or with two spines and median apophysis circular (Fig. 178) 40
40(39). Proximal end of median apophysis with one spine (Figs. 14, 244, 338, 399) 41
– Proximal end with two or three spines close together (Figs. 166, 183, 234, 239) 44
41(40). One spine on each end of median apophysis and a distal lobe (Fig. 14); Peru (Map 2) .... *tiganus*
– Median apophysis with one or two spines (Figs. 244, 338, 399) 42
42(41). Embolus a large counterclockwise structure in left palpus (Fig. 399); southern U.S., California to Colombia (Map 5) .... *detrimentosus*
– Embolus hidden or otherwise (Figs. 244, 338) 43
43(42). Median apophysis round (Fig. 244); legs with ventral black lines (Fig. 242); Mexico to Honduras (Map 3) .... *lineatipes*
– Median apophysis elongate (Fig. 338); legs without lines; Costa Rica (Map 5) .... *selva*
44(40). Median apophysis with two equal-sized spines (Fig. 234); eastern U.S., California to Ecuador (Map 3) .... *pegnia*
– Median apophysis otherwise 45
45(44). Median apophysis with three equal-sized spines (Fig. 239); eastern U.S., Mexico (Map 3) .... *thaddeus*
– Median apophysis otherwise 46
46(45). Filamentous embolus encased in a large transverse wrapper (Fig. 320); São Paulo State, Brazil (Map 3) .... *abeicus*
– Embolus otherwise 47
47(46). Base of conductor surrounded by embolus branches (Figs. 178, 183); Brazil 48
– Base on conductor free (Figs. 166, 172); Colombia, Peru 49
48(47). Median apophysis with pair of proximal spines, a blunt spine distally (Fig. 178); southern Brazil (Map 3) .... *stabilis*
– Median apophysis with one proximal spine and a distal forked spine (Fig.

183), Minas Gerais, Brazil (Map 3) ... *fronki*

49(47). Embolus laterally convex (Fig. 166); Andes, Colombia to Bolivia (Map 3) ... *meropes*

– Embolus laterally concave (Fig. 172); Peru (Map 3) ... *koepckeorum*

50(39). Median apophysis large, shape of half a disc (Fig. 325); southern Brazil (Map 3) ... *iguacu*

– Median apophysis otherwise ... 51

51(50). Distal end of median apophysis truncate, or with a "fish-tail" (Figs. 21, 208, 271) ... 56

– Distal end a point or fleshy expansion (Figs. 157, 275, 294, 302) ... 52

52(51). Median apophysis short with distal point as in Figure 157; Colombia (Map 2) ... *jamundi*

– Median apophysis otherwise ... 53

53(52). Distal end of median apophysis with a prong (Fig. 275); southern Brazil, Bolivia to Argentina (Map 3) ... *uniformis*

– Median apophysis otherwise ... 54

54(53). Embolus cone-shaped (Fig. 311); widespread (Map 4) ... *guttatus*

– Embolus curled or twisted (Figs. 294, 299) ... 55

55(54). Embolus with distal curl; median apophysis distally wide (Figs. 299, 302); widespread (Map 4) ... *venatrix*

– Embolus with twists; median apophysis distally narrow (Fig. 294); Espírito Santo, Rio de Janeiro States, Brazil (Map 3) ... *tijuca*

56(51). Chile, and Argentine Andes (Map 3) ... 57

– America, other than Chile, and Argentine Andes ... 61

57(56). Embolus with two "horizontal" notches as in Figures 249, 253 ... 58

– Embolus otherwise ... 59

58(57). Double spine of median apophysis with long narrow neck (Fig. 249) ... *talca*

– Double spine of median apophysis with short wide neck (Fig. 253) ... *concepcion*

59(57). Embolus with two convex lateral lobes as in Figure 271 ... *titirus*

– Embolus otherwise ... 60

60(59). Embolus convex laterally; double spine of median apophysis with short neck (Fig. 261) ... *huahun*

– Embolus concave laterally; double spine of median apophysis with long neck (Fig. 266) ... *alhue*

61(56). Palpus as in Figure 208; Mexico, Central America (Map 3) ... *expletus*

– South America ... 62

62(61). Median apophysis more than twice as long as wide, never U-shaped (Figs. 15, 41) ... 70

– Median apophysis about as long as wide or U-shaped (Figs. 68, 75, 121, 126, 136) ... 63

63(62). Brazil, Paraguay to Argentina ... 66

– Colombia to Peru ... 64

64(63). Conductor stalked (Figs. 136, 137); Peruvian mountains (Map 2) ... *urubamba*

– Conductor otherwise (Figs. 127, 152) ... 65

65(64). Conductor square (Fig. 127); Ecuadorian mountains (Map 2) ... *carchi*

– Conductor narrow (Fig. 152); Colombian, Ecuadorian mountains (Map 3) ... *granadensis*

66(63). Terminal apophysis bent on itself; embolus bulky (Fig. 121); Rio de Janeiro State, Brazil (Map 2) ... *pico*

– Terminal apophysis otherwise; embolus rod-shaped (Figs. 46, 48, 68, 70, 75, 77, 82, 84) ... 67

67(66). Median apophysis U-shaped; embolus straight (Figs. 46, 48); southern Brazil to Argentina (Map 2) ... *blumenau*

– Median apophysis otherwise; embolus straight or bent (Figs. 68, 75, 84) ... 68

68(67). Embolus straight (Figs. 68, 70); southern Brazil, Paraguay (Map 2) ... *vincibilis*

– Embolus bent (Figs. 77, 84) ... 69

69(68). Terminal apophysis shorter than subterminal as in Figure 77; embolar lamella with thick base set off from thin branch (Figs. 76, 77); Minas Gerais, Brazil, to Argentina (Map 2) ... *corporosus*

– Terminal apophysis as long as subterminal apophysis as in Figure 84; embolar lamella with base not set off, but grading into terminal branch (Figs. 83, 84); Espírito Santo State, Brazil, to Buenos Aires Province (Map 2) ... *workmani*

70(62). Tail of median apophysis mitten-shaped with an "upper" tooth (Fig. 15); São Paulo State, Brazil, (Map 2) ... *castilho*

– Tail of median apophysis otherwise ... 71

71(70). "Fish-tail" of median apophysis with a "lower" tooth (Fig. 40); embolar lamella d-shaped in ventral view (Fig. 41); northern Argentina (Map 2) ... *aurantiifemuris*

– "Fish-tail" without lower tooth, or if with tooth, embolar lamella not d-shaped ... 72

72(71). Embolar lamella complex, with middle portion in mesal view club-shaped (Fig. 131); Ecuadorian mountains (Map 2) ... *penai*

– Embolar lamella relatively simple (Figs. 21, 56, 116) ... 73

73(72). Embolus rod-shaped (Figs. 57, 63, 91) ... 75

– Embolus otherwise and with distal notch facing cymbium (Figs. 23, 34, 116) ... 74

74(73). Median apophysis narrowing laterally;

conductor curved around bulky embolus (Fig. 116); Mato Grosso, Brazil (Map 2) .... *xavantina*
– Median apophysis widening at lateral end (Fig. 21); conductor may cover narrow embolus (Fig. 21); widespread (Map 2) .... *bogotensis*

75(73). Tip of embolus some distance from lamella, the space in between V-shaped (Fig. 57); terminal apophysis hanging down toward embolus (Fig. 57); Espírito Santo State, Brazil, to Argentina (Map 2) .... *omnicolor*
– Tip of embolus close to lamella, the space in between oval (Figs. 63, 91); terminal apophysis otherwise (Figs. 63, 89) 76

76(75). Subterminal apophysis grooved (Figs. 89, 91); southern Brazil, Paraguay to Argentina (Map 2) .... *lathyrinus*
– Subterminal apophysis smooth (Figs. 61, 63); Bahia State, Brazil, to Argentina (Map 2) .... *unanimus*

Araneus andrewsi (Archer) Map 2

Aranea andrewsi Archer, 1951a: 31, figs. 63, 64, 82, ♀, ♂. Male holotype from Claremont, California, in AMNH.
Araneus andrewsi:—Levi, 1971: 146, figs. 27–33, ♀, ♂.

Distribution. Oregon to southern California along coastal plain.

Additional Record. MEXICO, *Baja California Norte:* 1.6 km S Miller's Landing, 6 July 1973, ♀ (S. C. Williams, CAS).

Araneus gemmoides Chamberlin and Ivie Map 2

Araneus gemmoides Chamberlin and Ivie, 1935: 22, pl. 10, fig. 80, ♀. Female holotype from Salt Lake City, Utah, in AMNH. Levi, 1971: 171, figs. 195–202, ♀, ♂.

Distribution. From British Columbia, Canada, to Michigan south to California and Alabama with a record on Isla San Lorenzo, Baja California Norte, Mexico (Levi, 1971).

Araneus sinistrellus (Roewer) Figures 5–8; Map 2

Aranea sinistra F. P.-Cambridge, 1904: 510, pl. 48, fig. 21, ♀. Two female syntypes from Omilteme [Omiltemi, 16 km WSW of Chilpancingo, Guerrero, 2600 m], Mexico, in BMNH, examined. Not *Epeira sinistra* (Thorell, 1873).
Araneus sinister:—Petrunkevitch, 1911: 316. Bonnet, 1955: 600.
Aranea sinistrella Roewer, 1942: 852. New name because *Aranea sinistra* preoccupied.

Note. I follow Roewer since Thorell's name is currently also placed in *Araneus* (Bonnet, 1955).

Description. Female. Carapace orange, hairy; eyes in lighter patches, rim of thorax lighter. Labium and endites brown. Sternum orange-brown. Coxae lighter orange-brown; legs orange ringed darker orange. Dorsum of abdomen with anterior median white cardiac mark, light orange without pattern, sclerotized spots dark brown (Fig. 7). Venter with black marks between epigynum and spinnerets (Fig. 8). Posterior median and lateral eyes 0.8 diameter of anterior median eyes. Anterior median eyes 1.5 their diameter apart, 4.5 from laterals. Posterior median eyes their diameter apart, 5 from laterals. Abdomen with pointed humps. Total length 16 mm. Carapace 8.3 mm long, 7.3 wide. First femur 9.6 mm, patella and tibia 11.5, metatarsus 7.5, tarsus 3.2. Second patella and tibia 10.7 mm, third 6.7, fourth 10.2.

The unknown male presumably has two hooks at the lateral end of the median apophysis, as do other species close to *A. cavaticus*.

Variation. Total length varies from 16 to 22 mm. The scape of the type specimen is wider at the tip and more rounded than the one illustrated (Fig. 5).

Diagnosis. Araneus sinistrellus is close to *A. cavaticus* (Keyserling) (Levi, 1971, figs. 187–194) of the eastern United States, having a wide triangular scape covering almost the entire base (Fig. 5) but unlike that of *A. cavaticus*, the scape is flat with the rim indistinct (Figs. 5, 6).

Natural History. If the habits of *A. sinistrellus* are the same as those of its relatives, it will be found on cliffs and buildings.

Record. MEXICO *Hidalgo:* 16 to 40 km

S Jacala, July 1956, 8 ♀, 3 imm. (V. Roth, W. J. Gertsch, AMNH).

Araneus tiganus (Chamberlin)
Figures 9–14; Map 2

Aranea tigana Chamberlin, 1916: 251, pl. 19, fig. 2, ♂ Male holotype from Lucma, 6000 ft (2000 m), Cusco, Peru, in MCZ, examined. Roewer, 1942: 854

Araneus tiganus:—Bonnet, 1955: 613.

Description. Female from Baños, Ecuador. Carapace dark brown with white down. Chelicerae, endites, labium, sternum dark brown. Coxae orange; legs orange with dark brown rings. Dorsum of abdomen dark brown, lighter in center with a pair of white marks anteriorly and darker irregular marks on sides (Fig. 12); venter dark dusky with a light band on each side (Fig. 13). Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.6. Anterior median eyes 0.8 diameter apart, 1.2 from laterals. Posterior median eyes 0.5 their diameter apart, 2.5 from laterals. Abdomen subspherical. Total length 10.3 mm. Carapace 4.6 mm long, 3.6 wide. First femur 4.5 mm, patella and tibia 5.7, metatarsus 4.4, tarsus 1.5. Second patella and tibia 4.8 mm, third 3.1, fourth 4.6.

Male holotype. Carapace orange, sides of thorax dusky. Labium, endites dark dusky. Sternum orange. Coxae light orange; legs light orange with indistinct darker orange rings. Dorsum of abdomen with light area, sides and posterior dusky; venter dusky in center, spinnerets brown. A median longitudinal line in thoracic depression. Posterior median and anterior lateral eyes 0.8 diameter of anterior medians, posterior laterals 0.7 diameter. Anterior median eyes slightly less than their diameter apart, 1 from laterals. Posterior median eyes 0.6 their diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with short strong macrosetae. Abdomen oval. Total length 5.2 mm. Carapace 2.9 mm long, 2.3 wide. First femur 3.6 mm, patella and tibia 4.6, metatarsus 3.5, tarsus 1.2. Second patella and tibia 3.4 mm, third 1.9, fourth 2.7.

Variation. The scape of the epigynum is broken off in most specimens (Fig. 10). Total length of females 6.7 to 10.3 mm, of males 5.2 to 6.7.

Diagnosis. The female differs from all other *Araneus* species by having the scape of the epigynum without annuli (Fig. 9). It is the only species in Ecuador and Peru found with the scape torn off with a remaining base that differs from that of *A. bogotensis* (Figs. 17, 24) by the wide scar of the torn scape (Fig. 10). The male's median apophysis of the palpus has a proximal spine as well as one lateral, above which is a lobe (Fig. 14).

Araneus lechugalensis (Keyserling), as illustrated by Keyserling, is quite similar to *A. tiganus*, but the female of *A. tiganus* appears to be smaller. The type of *A. lechugalensis* from Lechugal, Peru, has been lost and no specimens were found that matched the illustration exactly (the scape of the epigynum appears torn off). *A. lechugalensis* may be *A. meropes*.

→

Figures 1–4 *Araneus* genital morphology. 1–4. *A. bogotensis* (Keyserling). 1. Epigynum, ventral. 2. Epigynum, posterior. 3, 4. Male, left palpus, expanded. 3. Subventral. 4. Dorsal. 1, 2 (Dpto. César, Colombia). 3, 4 (Dpto. Valle, Colombia).

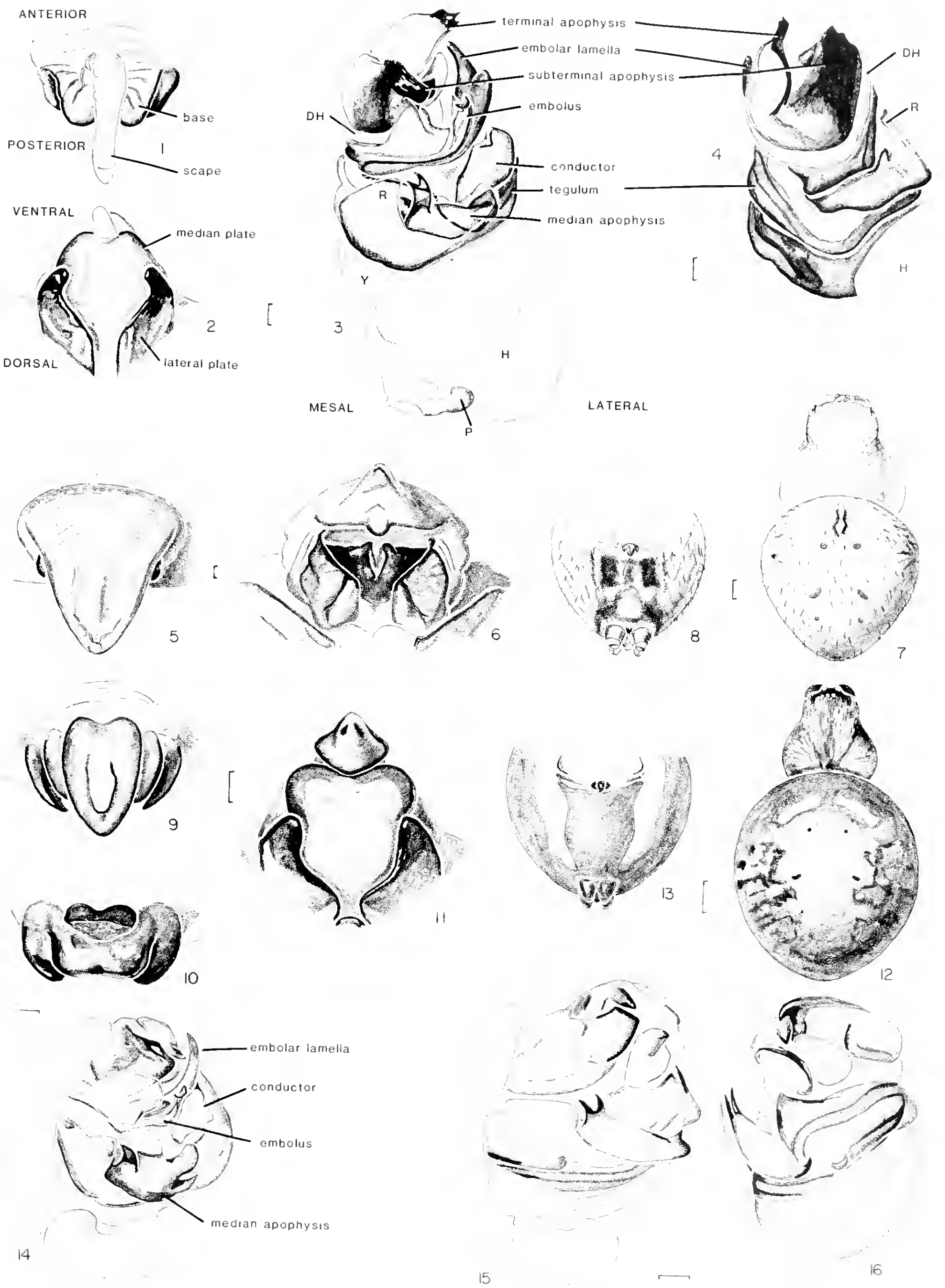
Figures 5–8. *A. sinistrellus* (Roewer), female. 5. Epigynum, ventral. 6. Epigynum, posterior. 7. Dorsal. 8. Abdomen, ventral.

Figures 9–14 *A. tiganus* (Chamberlin). 9–13. Female. 9. Epigynum, ventral. 10. Epigynum, scape torn. 11. Epigynum, posterior. 12 Dorsal. 13. Abdomen, ventral. 14. Male palpus, mesal.

Figures 15, 16 *A castilho* n. sp., male palpus. 15. Mesal. 16. Ventral.

Abbreviations DH, distal hematodocha. H, hematodocha. P, paracymbium. R, radix. Y, cymbium.

Scale lines 1.0 mm, genitalia 0.1 mm.


ANTERIOR
base
POSTERIOR
1
scape
VENTRAL
median plate
2
DORSAL
lateral plate
terminal apophysis
embolar lamella
subterminal apophysis
DH
embolus
conductor
tegulum
R
median apophysis
Y
3
H
MESAL
P
LATERAL
4
DH
R
H
5
6
8
7
9
11
13
10
12
embolar lamella
conductor
embolus
median apophysis
14
15
16

Distribution. Ecuador and Peruvian mountains, 1000–2200 m (Map 2).

Records. ECUADOR *Tungurahua:* Baños, 1600–2000 m, many specimens (AMNH, CAS, MCZ); Pastaza Valley between Baños and Mera, 1000–1700 m, Jan.–Mar. 1949, 10 ♀, 2 ♂ (W. C. MacIntyre, AMNH). *Loja:* Zamora, 1800–2200 m, 28 Oct. 1977, ♀ (L. Peña, AMNH). PERU *Pasco:* Oxapampa, 2500 m, 12 June 1986, 2 ♀ (D. Silva D., MNHSM). *Junín:* Pumamarca, 2 ♀ (K. Jelski, J. Sztolcman, PAN).

Araneus castilho new species
Figures 15, 16; Map 2

Holotype. Male holotype from Castilho, Est. São Paulo, Brazil, 17 Oct. 1964 (Exped. Dpto. Zool.), in MZSP no. 3885. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace, chelicerae, sternum, legs orange. Dorsum of abdomen white, sides whitish without white pigment spots. Head narrow and eyes small. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 1.4 diameters apart, 1.5 from laterals. Posterior median eyes 1.5 diameters apart, 3.3 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with a large distal macroseta and some short macrosetae. Abdomen oval, pointed behind. Total length 5.0 mm. Carapace 2.4 mm long, 2.0 wide. First femur 3.2 mm, patella and tibia 4.1, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.2 mm, third 1.8, fourth 2.7.

Diagnosis. The male is distinguished by the relatively long median apophysis (Fig. 15), and, in ventral view, the mushroom-shaped conductor and round embolar lamella (Fig. 16). The unusually small eyes are distinctive and may make it possible to match the male with a female.

Araneus bogotensis (Keyserling)
Figures 1–4, 17–36; Map 2

Epeira bogotensis Keyserling, 1864: 88, pl. 4, figs. 1–6, ♀, ♂. Female lectotype and male and several female paralectotypes here designated from Santa Fé de Bogota, New Granada [Bogotá, Colombia], in BMNH, examined. Keyserling, 1892: 167, pl. 8, fig. 124, ♀.

Epeira abunda Taczanowski, 1878: 152, pl. 1, fig. 7, ♀, ♂. Female lectotype here designated, female and male paralectotypes from Uaca Pistana [Huacapistana, Junín, 2500 m], Peru, in PAN, examined.

Aranea quechuana Chamberlin, 1916: 250, pl. 19, fig. 1, ♂. Male holotype from Huadquina, 5000 ft [1500 m, Dpto. Cusco, 13°07′S, 72°39′W], Peru, in MCZ, examined. Roewer, 1942: 850. NEW SYNONYMY.

Aranea abunda:—Roewer, 1942: 836.

Neosconella magna di Caporiacco, 1955: 351, fig. 33, ♀. Female holotype from Rancho Grande, Aragua, Venezuela, in collection of Univ. Central, Caracas, examined. NEW SYNONYMY.

Aranea bogotensis:—Roewer, 1942: 838.

Araneus abundus:—Bonnet, 1955: 419.

Araneus bogotensis:—Bonnet, 1955: 448.

Araneus quechuanus:—Bonnet, 1955: 580.

Description. Female from Dpto. Valle, Colombia. Carapace dark brown with white hair, eye region black, thoracic border white. Labium, endites, and sternum dark brown. Coxae light orange; legs ringed dark brown and orange. Dorsum of abdomen with brown and white pattern (Fig. 19); venter with a longitudinal light band on each side (Fig. 20). Posterior median eyes and anterior lateral eyes 0.8 diameter of anterior median eyes, posterior lateral eyes 0.7. Anterior median eyes a little less than their diameter apart, 1.5 from laterals; posterior median eyes 0.6 their diameter apart, 2.2 from laterals. Abdomen spherical. Total length 12.0 mm. Carapace

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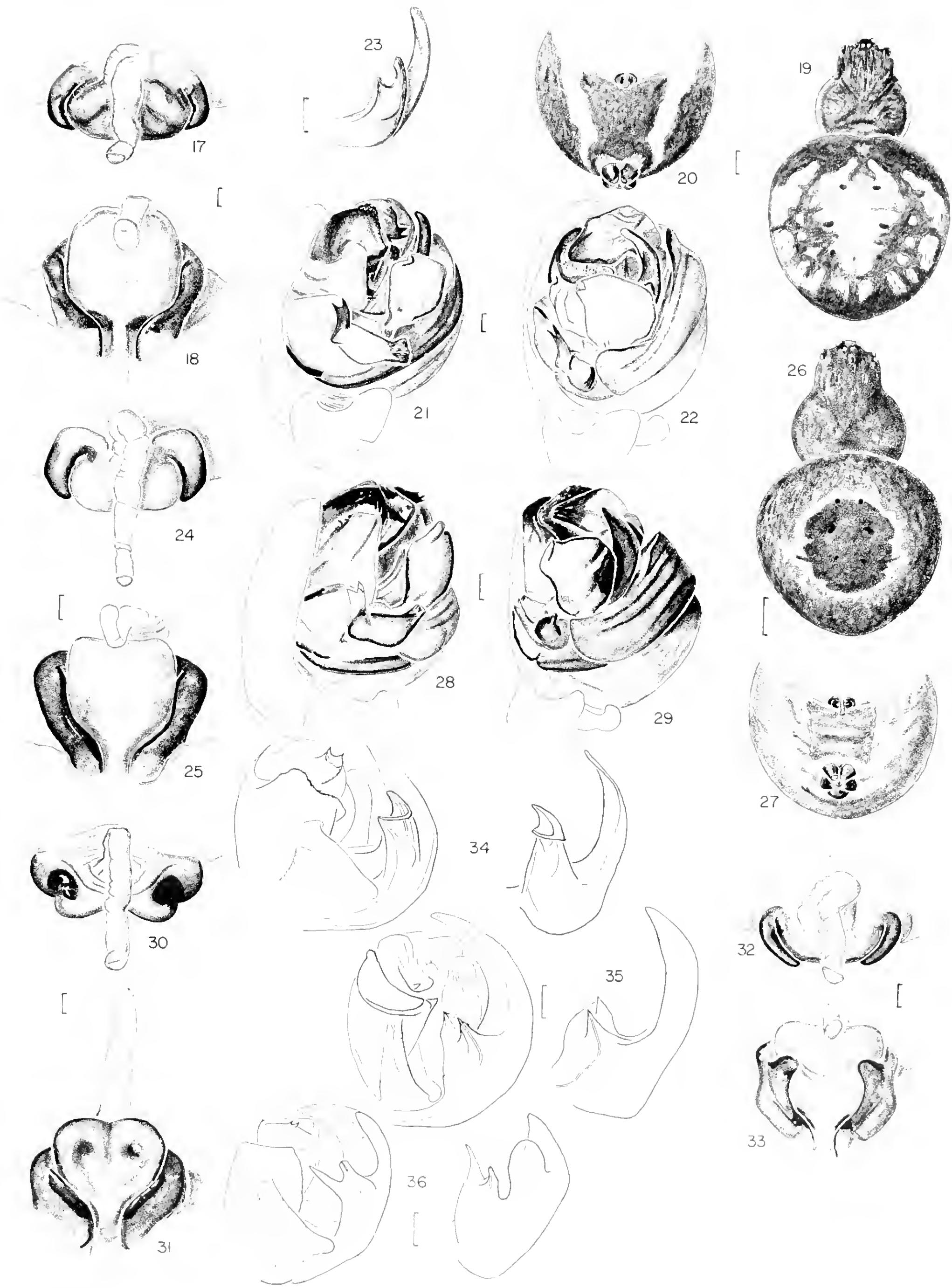
Figures 17–36. *Araneus bogotensis* (Keyserling). 17, 24, 30, 32. Epigynum, ventral. 18, 25, 31, 33. Epigynum, posterior. 19, 26. Female. 20, 27. Female, abdomen, ventral. 21, 22, 28, 29, 34–36. Male, left palpus. 21, 28. Mesal. 22, 29. Ventral. 34–36. Outline of embolus, subterminal and terminal apophyses mesal, and embolus ventral. 34. With embolus cap. 35, 36. Without cap. 35, 36. Doubtful determinations. 17–21, 23 (Dpto. Valle, Colombia). 22 (Pichincha Prov., Ecuador). 24–27, 30, 31. Doubtful species (Volcán Puracé area, Colombia). 28, 29 (Quito, Ecuador). 32, 33 (Bolivia). 34 (Sierra Nevada de Santa Marta, Colombia). 35 (Puracé area, Colombia). 36 (Quito, Ecuador).

Scale lines 1.0 mm, genitalia 0.1 mm.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4.8 mm long, 3.9 wide. First femur 4.8 mm, patella and tibia 5.7, metatarsus 4.3, tarsus 1.5. Second patella and tibia 5.2 mm, third 3.2, fourth 4.7.

Male from Dpto. Valle, Colombia. Carapace orange, dorsum of abdomen black anteriorly on each side with seven pairs of dark transverse marks; sides with black mark; otherwise colored as female. Posterior median and lateral eyes 0.7 diameter of anterior medians. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.6 diameter apart, 2.5 from laterals. First coxa with hook. Second tibia slightly thicker than first. Total length 7.4 mm. Carapace 3.6 mm long, 2.9 wide. First femur 4.4 mm, patella and tibia 5.4, metatarsus 4.0, tarsus 1.5. Second patella and tibia 4.2 mm, third 2.5, fourth 3.5.

Variation. Total length of females 6.8 to 12.8 mm, in Colombia 7.7 to 12.8, in Ecuador and Peru 7.5 to 12.3, in Brazil 6.8 to 9.5. Total length of males 4.5 to 7.9 mm, in Colombia 4.5 to 6.7, in Ecuador and Peru 7.3 to 7.9. The largest individuals came from Volcan Puracé area in southern Colombia. These Puracé specimens were very dark, lacking ventral light bands on the abdomen (Figs. 26, 27).

The epigyna of females from central and southern Colombia lack the curved prongs of the lateral plates on the posterior face, which are present in females from all other areas. The female lectotype of *Epeira bogotensis* lacks these prongs (Fig. 18); the female lectotype of *Epeira abunda* has them (Figs. 2, 33). The median plate of the epigynum is square in most females (Fig. 25), but in southern Colombia and Ecuador some individuals have a triangular median plate (Fig. 31). A lobe is present between the lamella and the embolus in the palpus of some males from southern Colombia (normally hidden behind the conductor, Fig. 36). The lamella may be thick in some males from Ecuador. The embolus of the male palpus has two tips: the lateral sclerotized tip contains the duct and varies little (Figs. 34, 36). The other, softer tip, may be drawn out and larger in some specimens than in others (Figs. 34–36). Between the embolus and subterminal apophysis is an oval, curved, stippled sclerite; in no two males from the mountains of Colombia and Ecuador is it quite the same shape (Figs. 34, 35). The subterminal apophysis is rounded and shiny in many male palpi, in others it has a groove; in no two males does it have quite the same shape.

None of these characters of variation overlap. When I started out with only few specimens, I thought there were several species. Additional collections showed that there were intermediates: females with short prongs of the lateral plates, females with the posterior plate not quite triangular, individuals with indistinct ventral marks, and males with a tiny lobe between lamella and embolus. There are not many males in the collections, and few were collected with females. Most available collections come from Ecuador and southern Colombia, very few from the Peruvian mountains.

In southern Colombia, populations of this widespread species seem to be partly isolated and thus are unusually variable. Collection of a large series would make a more detailed study possible.

Diagnosis. Araneus bogotensis is separated from *A. granadensis* (Figs. 146, 147) by having the posterior plate of the epigynum square (Fig. 18), and the conductor of the palpus as wide as long (Figs. 21, 22). In *A. granadensis*, the posterior plate is longer than wide (Fig. 147) and has the conductor of the male palpus longer than wide (Fig. 150). *Araneus granadensis* appears to have openings in the lateral plate of the epigynum seen in both ventral and posterior view (Figs. 146, 147); *A. bogotensis* does not (Figs. 17, 18). *Araneus granadensis* has the scape equal in width and straight (Fig. 146), while the scape of *A. bogotensis* is usually slightly bent and wider in some parts than in others (Figs. 17, 24, 30).

Natural History. The species has been collected on low vegetation along roadsides in Colombia, on low shrubs around

an open bog on Cerro Neblina, Venezuela, and from webs on a cliff face in Peru, at elevations from 120 to 4000 m.

Distribution. From Venezuela and Colombia to Bolivia in the Andes and in the states of Espírito Santo to São Paulo, Brazil; common in Colombia and Ecuador (Map 2).

Records. VENEZUELA *Aragua:* Rancho Grande (AMNH, MCZ). *Amazonas:* Neblina Massif, 15 km NNW Pico Phelps (MCZ); Cerro de la Neblina, 1690–2100 m (USNM). *Mérida:* nr. La Azulita (MCZ). COLOMBIA *Magdalena:* Sierra Nevada de Santa Marta, 1500–1900 m (MCZ, JAK, SMF). *César:* Sierra de Perijá, 1500–1600 m (AMNH). *Santander:* Río Suárez, 800–1000 m (AMNH). *Antioquia:* Medellín, 2800 m (MHNM, MCZ); Laguna Guarne, 2700 m (MHNM); Urrao (MHNM); La Estrella, 2000 m (MCZ); Sabaneta, 1600 m (MHNM); San Vincente (MHNM). *Boyacá:* Paramo Alto Belen (MCZ). *Cundinamarca:* Monterredondo, 1200 m (MCZ); Paramo de Chingaza, 3100 m (MCZ); nr. Sasaima (DU); Bogotá (MCZ, AMNH). *Caldas:* nr. Manizales, 2300 m (MCZ). *Meta:* Villavicencio, 400–920 m (AMNH, CAS, MCZ). *Valle:* Yotoco, 1500 m; Lago Calima, 1400 m; nr. Cali, 1000 m; Pichinde, 1700 m; above Fidelia, 2000 m; Arriba de Salidato, 1800 m; above Habana; nr. Queremal (all MCZ); E Caicedonia (CAS); 10 km W Cali, 1630 m (CAS); Cali (AMNH). *Huila:* 19 km E Sta. Leticia, 2300 m (MCZ); Paramo Puracé, 3400 m (MCZ, JAK). *Cauca:* nr. Silvia, betw. Mondomo and Piendamó (both MCZ). *Nariño:* La Cruz, 2450 m; La Planada, 1800 m (both MCZ); 6.5 km S La Unión (CAS). *Putumayo:* Sibundoy, 2200–2600 m (MCZ). ECUADOR *Pichincha:* Quito, 2500 m (CAS, MECN); Río Pilatón (MCZ); 16 km SE Santo Domingo, 680 m (MCZ); Machachi (BMNH); Machachi to Pedregal (BMNH); Tandapi, 1300–1500 m (MCZ); Las Palmeras, 2000 m (MECN); Niebli (MECN); Chiriboga (MECN); Cumbaya (MECN); 45 km S Quito (CAS); Pasochoa (MECN). *Napo:* Río Topo (CAS); E Papallacta (AMNH); 6.5 km S Baeza, 1800 m (MCZ). *Cotopaxi:* Macuchi (CAS); W Pilaló (AMNH). *Tungurahua:* Baños, 1850–2000 m (MCZ, CAS); Runtun, Baños, 2300 m (AMNH); Mt. Tungurahua, 3800 m (AMNH). *Chimborazo:* Volcán Chimborazo, 3600–4000 m (BMNH); 48 km S Alausí (CAS). *Bolivar:* Balzapamba (AMNH). *Morona-Santiago:* Wakani, Chiguasa (MCZ). *Azuay:* Lago Zurucuchi, 18 km W Cuenca (CAS); Reserva de Lagunas (MECN); Tinajillas, 3100 m (MCZ). *Loja:* Zamora to Loja, 2000–2500 m (MCZ); Cord. de Celica, Alamor, 1100–2200 m (AMNH). PERU *Piura:* Ayabaca (CAS). *Cajamarca:* Hacienda Taulís (MHNSM); Montaña di Nancho, 3000 m (PAN); Chota, 2600–2700 m (CAS). *La Libertad:* Yalen, 2900 m (MHNSM); Huamachuco, 3200 m (CAS). *Ancash:* Puma nr. Huaraz, 4000 m (AMNH). *Huánuco:* Carpish, Huánuco Mts. (CAS); Sariapamp, 3600 m (CAS). *Pasco:* Oxapampa (CAS, MHNSM). *Lima:* Río Cañete, betw. Yauyos and Magdalena, 2800 m (CAS). *Junín:* Huacapistana (CAS); Maraynioc (PAN); Viena (BMNH); Tarma (CAS); Joras (MHNSM); Amable María (PAN); Pumamarca, 2000 m (PAN). *Cusco:* Machupicchu (AMNH, USNM); Lucma, 2000 m (MCZ); Torontoy Canyon, 2000–2200 m (AMNH); Río Marcapata (BMNH); Atalaya (USNM). *Puno:* Limbani, Carabaya, 2900 m (BMNH). *Ayacucho:* San Miguel, 2000 m (MCZ). BOLIVIA *La Paz:* Yungas del Palmar (ZSM); Tarata, Río Zongo, 3200 m (AMNH); Río Coroico, 1400–1600 m (AMNH); betw. Yungas and La Paz (IRSNB). BRAZIL *Espírito Santo:* Castelo (AMNH). *Rio de Janeiro:* Serra dos Órgãos, 1850 m (MCZ); Itatiaia, 1200–1400 m (AMNH, MZSP); Santa Maria Madalena (MNRJ). *São Paulo:* Bosque de Saúde, São Paulo (MZSP); Itaim (MZSP); São José do Barreiro, S Bocaina, 1960 m (AMNH).

Araneus aurantiifemuris (Mello-Leitão) new combination
Figures 37–41; Map 2

Metepeira aurantiifemuris Mello-Leitão, 1942: 402, figs. 21, 22, ♀. Female holotype from Tirol, Chaco Prov., Argentina, in MLP, examined. Brignoli, 1983: 275.

Description. Female from Córdoba. Carapace orange with a median darker streak. Chelicerae, labium, endites orange. Sternum orange. Coxae orange; legs orange with a dark ring on distal end of fourth tibia; fourth metatarsus and tarsus dark. Dorsum of abdomen with white pigment spots (Fig. 39); venter with a white square between epigynum and spinnerets consisting of small white spots. Posterior median eyes same diameter as anterior medians, anterior laterals 0.8 diameter, posterior laterals 1. Anterior median eyes 1.3 diameters apart, 1.4 from laterals. Posterior median eyes 0.6 their diameter apart, 2 from laterals. Abdomen spherical (Fig. 39). Total length 6.0 mm. Carapace 2.5 mm long, 2.1 wide. First femur 2.8 mm, patella and tibia 3.1, metatarsus 2.5, tarsus 0.8. Second patella and tibia 2.6 mm, third 1.6, fourth 2.3.

Male from Córdoba. Color as in female, including white pigment spots on abdomen, but without dark rings on fourth legs. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.5 diameter, posterior laterals 0.5. Anterior median eyes their diameter apart, 0.9 from laterals. Posterior median eyes 0.6 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia only slightly thicker than first, without short macrosetae. Abdomen oval. Total length 4.6 mm. Carapace 2.5 mm long, 1.9 wide. First femur 4.2 mm, patella and tibia 4.9, metatarsus 4.5, tarsus 0.9. Second patella and tibia 3.7 mm, third 1.8, fourth 2.7.

Diagnosis. Females have the median plate of the epigynum square in posterior view (Fig. 38) as in *A. bogotensis* (Fig. 25), females differ by their light coloration and especially the white pigment spots on the abdomen (Fig. 39). The male differs from *A. bogotensis* and others by the shape of the embolus lamella in lateral view of the palpus (Fig. 41) and the curved embolus partly hidden by the lamella in ventral view (Fig. 40).

Distribution. The species is known only from northern Argentina (Map 2).

Records. ARGENTINA *Corrientes:* Goya, Mar., Apr. 1958, 2 ♀ (J. Scarpa, MACN). *Córdoba:* Calamuchita, Jan. 1955, ♀, ♂ (Viana, MACN).

Araneus blumenau new species
Figures 42–48; Map 2

Holotype. Female holotype and male paratype from Blumenau, Est. Santa Catarina, Brazil, ca. 1910 (E. Reimoser), in MZSP, ex MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace with head dark orange, thorax lighter. Chelicerae proximally dark, distally light orange. Labium, endites, sternum orange. Coxae orange; legs orange with indistinct darker rings. Dorsum of abdomen greenish white, anteriorly darker on sides (Fig. 44); venter with median white patches (Fig. 45). Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.2 diameters apart, 1.4 from laterals. Posterior median eyes 0.6 diameter apart, 2.3 from laterals. Abdomen spherical, slightly wider than long (Fig. 44). Total length 7.7 mm. Carapace 2.8 mm long, 2.5 wide. First femur 2.9 mm, patella and tibia 3.4, meta-

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Figures 37–41. *Araneus aurantiifemuris* (Mello-Leitão). 37–39. Female. 37. Epigynum, ventral. 38. Epigynum, posterior. 39. Dorsal. 40, 41. Male, left palpus. 40. Mesal. 41. Ventral.

Figures 42–48. *A. blumenau* n. sp. 42–45. Female. 42. Epigynum, ventral. 43. Epigynum, posterior. 44. Dorsal. 45. Abdomen, ventral. 46–48. Male palpus. 46. Mesal. 47. Ventral. 48. Embolus, subterminal and terminal apophyses, mesal.

Figures 49–57. *A. omnicolor* (Keyserling). 49–54. Female. 49–51. Epigynum, ventral. 50, 52. Epigynum, posterior. 49, 50 (São Paulo, Brazil). 51, 52 (Paraná, Brazil). 53. Dorsal. 54. Abdomen, ventral. 55–57. Male palpus. 55. Mesal. 56. Ventral. 57. Embolus, without cap, subterminal and terminal apophyses and embolus with cap, right.

Scale lines. 1.0 mm, genitalia 0.1 mm.


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tarsus 2.8, tarsus 0.9. Second patella and tibia 3.0 mm, third 1.8, fourth 2.7.

Male from Blumenau. Cephalothorax in poor condition, but color as in female. Abdomen with dorsal white wedge-shaped mark pointing posteriorly, venter with a white band on each side from genital area to spinnerets, and some white spots behind genital groove. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes slightly less than 1 diameter apart, slightly less than 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with macrosetae. Abdomen oval, longer than wide. Total length 4.0 mm. Carapace 2.0 mm long, 1.1 wide. First femur 2.7 mm, patella and tibia 3.4, metatarsus 2.7, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.2, fourth 1.9.

Variation. The abdomen of a specimen from Uruguay is green. Total length of females 5.7 to 7.7 mm, of males 3.9 to 5.8.

Diagnosis. The female is lighter colored than is *A. bogotensis* and has the median plate of the epigynum in posterior view projecting ventrally, beyond the lateral plates, and the median plate wide dorsally (Fig. 43). The palpus differs from that of similar species by the U-shaped median apophysis, the long straight embolus (Figs. 46–48), and wide embolus lamella (Fig. 47).

Distribution. Southern Brazil to northern Argentina (Map 2).

Paratypes. URUGUAY *Río Negro:* Arroyo Negro, 15 km S Paysandú, 2 Jan. 1963, ♀ (R. G. van Gelder, AMNH). ARGENTINA *Salta:* Martín García, ♀ (Viana, MACN). *Santa Fé:* Delta de Paraná, Río Caraguatay, Apr. 1940, ♂ (F. Monrós, MACN). *Entre Ríos:* Victoria, Dec. 1964, ♂ (M. E. Galiano, MEG). *Buenos Aires:* Isla Martín García, ♀, ♂, 2 Dec. 1965 (M. E. Galiano, MEG); Sierra de la Ventana, Nov. 1954, ♀ (Fritz, MACN); "Guilures," ♂ (Viana, MACN); Buenos Aires, ♂ (1942) MACN).

Araneus omnicolor (Keyserling)
Plate 1; Figures 49–57; Map 2

Epeira omnicolor Keyserling, 1893: 210, pl. 10, fig. 155, ♀. Female holotype from Est. Espírito Santo, Brazil, in BMNH, examined.

Aranea omnicolor:—Roewer, 1942: 849.

Neosconella farinosa Mello-Leitão, 1941a: 152, pl. 1, fig. 2, 48, ♀. Female holotype from Salta, Argentina, in MLP, examined. NEW SYNONYMY.

?*Larinia albosigillata* Mello-Leitão, 1947: 247, fig. 13, imm. Immature holotype from Paranaí, Paraná, Brazil, in MHNC, examined. NEW SYNONYMY.

Araneus omnicolor:—Bonnet, 1955: 560.

Araneus farinosus:—Brignoli, 1983: 262.

Note. The female holotype of *A. farinosa* does not have the median bulge of the epigynum constricted anteriorly in ventral view, but has the diagnostic lobes on the lateral plates in posterior view.

Description. Female from São Paulo. Carapace orange with darker marks on head and sides of thorax (Fig. 53). Labium, endites dark brown; sternum dark brown with median anterior orange streak. Coxae orange; first to third legs with indistinct dark rings, fourth with contrasting rings. Dorsum of abdomen with indistinct transverse lines on the sides (Fig. 53); venter with black square (Fig. 54). Carapace with down. Posterior median eyes same diameter as anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes a little less than their diameter apart, 1.2 from laterals. Posterior median eyes 0.6 diameter apart, a little less than 2 from laterals. Abdomen oval, hairy. Total length 9.7 mm. Carapace 4.1 mm long, 3.5 wide. First femur 4.9 mm, patella and tibia 6.2, metatarsus 4.2, tarsus 1.4. Second patella and tibia 5.2 mm, third 2.9, fourth 4.5.

Male from São Paulo. Color as in female. Posterior median eyes 0.8 diameter of anterior median eyes, lateral eyes 0.6 diameter. Anterior median eyes their diameter apart, a little less than their diameter from laterals. Posterior median eyes 0.6 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first. Total length 6.7 mm. Carapace 3.6 mm long, 2.8 wide.

First femur 4.8 mm, patella and tibia 5.7, metatarsus 3.9, tarsus 1.2. Second patella and tibia 4.5 mm, third 2.4, fourth 3.5.

Note. Males and females have been collected together several times.

Variation. A photograph of a live female (Plate 1) shows the abdomen shaded brown with some red marks anteriorly and white marks posteriorly and on the sides. Total length of females 7.2 to 10.7 mm, of males 4.5 to 6.7. Although the area between the posterior median eyes is always light in color, the carapace is quite variable and may be dark or light in males and females. The scape of the epigynum may be nearly pointed (Fig. 49) or wide at the distal end (Fig. 51). The median plate in ventral view may be more or less bulging.

Diagnosis. The female can easily be separated from similar species by the 90° angle of the median lobes of the lateral plates and the oval, bulging median plate in posterior view (Figs. 50, 52). The median plate, unlike that of *A. lathyrinus* (Fig. 86) has no depressions. It has a variable number of dorsal transverse grooves and appears almost segmented (Figs. 50, 52), unlike that of *A. vincibilis* (Fig. 65).

The male can be separated from similar species by the relatively wide embolar lamella (Figs. 55, 56) and the gap between the tip of the embolus and the lamella (Fig. 57). Also, the terminal apophysis appears longer and seems to hang down toward the embolus tip (Figs. 55, 57).

Natural History. Specimens have been collected in a forest and in vegetation of a wet roadcut in Tijuca National Park and in an undisturbed tall forest in Paraguay.

Distribution. From Bahia state, Brazil, to Buenos Aires Province, Argentina (Map 2).

Records. BRAZIL *Bahia:* Bahia Galadea [?], ♀ (ZMK). *Minas Gerais:* Caxambu, ♀ (MCZ). *Rio de Janeiro:* Serra dos Orgãos, 1000–1800 m, 2 ♀ (MCZ); Pico da Tijuca, 500–950 m (MCZ); Parque Nac. Itatiaia, 1200–1400 m, ♀, ♂ (AMNH); Rio de Janeiro, ♀ (AMNH); Teresópolis, 2 ♀ (AMNH). *São Paulo:* São Paulo, Jardim Botânico, ♀, ♂ (MCZ, AMNH); Itu, ♂ (MCN); Nova Europa, ♀ (MZSP); Cocaia, ♀ (MZSP); Barueri, ♀ (MZSP). *Paraná:* Curitiba, 2 ♀ (MCN); Araucária, ♀ (MZSP). *Santa Catarina:* Pinhal, ♀ (AMNH). *Rio Grande do Sul:* Porto Alegre, 2♀, ♂ (MCN); Caxias do Sul, ♀ (MCN); Vacaria, ♂ (MCN); São Leopoldo, ♀ (MCN); Triunfo, 2♀ (MCN); Esmeralda, ♀ (MCN); Canela, 4♀ (MCN); Dois Irmãos, ♀ (MCN); Montenegro, ♀ (MCN); Caçapava do Sul, ♀ (MCN). PARAGUAY *Amambay:* Parque Nac. Cerro Corá, 2♀ (IBNP, MCZ). *Alto Paraná:* Km 12 de Stroessner, ♀ (IBNP). *Paraguarí:* Cerro Acahai, ♀ (IBNP). ARGENTINA *Salta:* Tabacal, ♀ (MACN). *Formosa:* Formosa, ♂ (MACN). *Buenos Aires:* Punta Lara, ♀ (MEG).

Araneus unanimus (Keyserling)
Plate 1; Figures 58–63; Map 2

Epeira unanima Keyserling, 1880: 306, pl. 4, fig. 9, ♀. Female holotype from Nova Friburgo, Est. Rio de Janeiro, Brazil, in BMNH, examined; 1892: 147, pl. 7, fig. 108, ♀.

?*Epeira biplagiata* Bertkau, 1880: 86, fig. 30. Immature specimens from São João del Rei (Minas Gerais) and Théresopolis (Teresópolis, Est. Rio de Janeiro), Brazil, lost. Not in Alexander König Museum, Bonn, Germany, SMF, IRSNB, BMNH. NEW SYNONYMY.

Aranea unanima:—Roewer, 1942: 855.

Aranea biplagiata:—Roewer, 1942: 837.

Araneus unanimus:—Bonnet, 1955: 625.

Araneus biplagiatus:—Bonnet, 1955: 443

Note. The white patches on the immature specimens of *E. biplagiata* illustrated by Bertkau suggest that they belong to this species.

Description. Female from Rio Grande do Sul (MNRJ). Carapace orange. Chelicerae, labium, endites orange. Sternum, legs orange. Dorsum of abdomen with white patches (Fig. 60); venter white around anterior margin. Posterior median eyes same diameter as anterior medians, anterior laterals 1 diameter, posterior laterals 0.8. Anterior median eyes 1.2 diameters apart, 1.4 from laterals. Posterior median eyes 0.5 diameter apart, 2.4 from laterals. Abdomen spherical, soft (Fig. 60). Total length

7.5 mm. Carapace 3.5 mm long, 3.0 wide. First femur 4.0 mm, patella and tibia 4.8, metatarsus 3.5, tarsus 1.3. Second patella and tibia 3.9 mm, third 2.6, fourth 3.7.

Male from Rio Grande do Sul. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 1 diameter apart, 1 from laterals. Posterior median eyes 0.6 diameter apart, 2.3 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with long and short macrosetae. Abdomen oval. Total length 7.4 mm. Carapace 3.8 mm long, 3.1 wide. First femur 4.6 mm, patella and tibia 5.7, metatarsus 3.7, tarsus 1.1. Second patella and tibia 4.4 mm, third 2.6, fourth 3.5.

Variation. Total length of females 6.7 to 10.1 mm, of males 4.6 to 5.9. The photograph of a living female (Plate 1) shows the carapace and legs to be green, the abdomen glossy light green with a reddish area on each side. Some specimens have a brown patch on the chelicerae or the head, and a few have irregularly spaced brown rings on legs.

Diagnosis. This species differs from related ones in having almost no black pigment, even around the eyes. In ventral view the epigynum has a pair of slits whose anterior end is covered by a hood (Fig. 58) and in posterior view the median plate is almost pentagonal in shape (Fig. 59).

The palpus has a relatively long, slightly curved embolus approaching a lobe of the edge of the wide lamella (Fig. 63), the subterminal apophysis is swollen and entire (Fig. 63), and the conductor is twice as long as wide (Fig. 62).

Natural History. The species has been found in a forested area in the Tijuca National Park and in a tall undisturbed forest in Paraguay.

Distribution. From Bahía State, Brazil, in the north to Río Negro Province, Argentina, in the south (Map 2).

Paratypes. BRAZIL *Bahia:* Salvador, ♀ (AMNH). *Rio de Janeiro:* Rio de Janeiro ♀ (AMNH, MNRJ); Parque Nac. Tijuca, ♀ (MCZ); Petrópolis, ♀ (MNRJ). *São Paulo:* Itu, ♂ (MZSP, AMNH); Caraguatatuba, ♀, ♂ (MZSP); Boracéia, ♀, ♂ (MZSP); São Paulo, ♀ (MZSP, AMNH); Serra Negra ♀, ♂ (MZSP); Cocaia, ♀, ♂ (MZSP); Santo Amaro, ♀ (MZSP); Alto da Serra, ♀ (MZSP); Ilha da Vitória, ♀ (MZSP); S. Bernardo, ♀, ♂ (MZSP). *Paraná:* Curitiba, ♀, ♂ (MZSP, MNRJ); Vila Velha, ♀, (MZSP). *Santa Caterina:* Corupá, ♀ (AMNH); Pinhal, ♀ (AMNH); Morro dos Conventos Araranguá, ♂ (MCN). *Rio Grande do Sul:* São Borja Garruchos, ♂ (MCN); Tramandaí, ♂ (MCN); Canela, ♀, ♂ (MCN); São Leopoldo, ♀ (MZSP); Porto Alegre, ♀, ♂ (MCN); São Jerônimo, ♂ (MCN); Rio Grande, ♂ (MCN); General Câmara, ♀ (MCN); Pelotas, ♀, ♂ (AMNH, MCN); Novo Hamburgo, ♀ (MCN); Vila Oliva, Caxias do Sul, 2♀, ♂ (MCN); Berto Ciro Canoas, ♂ (MCN). PARAGUAY *Paraguarí:* Ybycuí, ♀, ♂ (IBNP). *Caazapá:* Parque Nac. Caaguazú, 2♀ (IBNP). ARGENTINA *Misiones:* Cataratas de Iguacu, ♀ (MEG); Tobuna, ♀ (AMNH). *Formosa:* Est. Gaiacolá, R. Pilagá, ♂ (MACN). *Río Negro:* El Bolsón, ♂ (AMNH).

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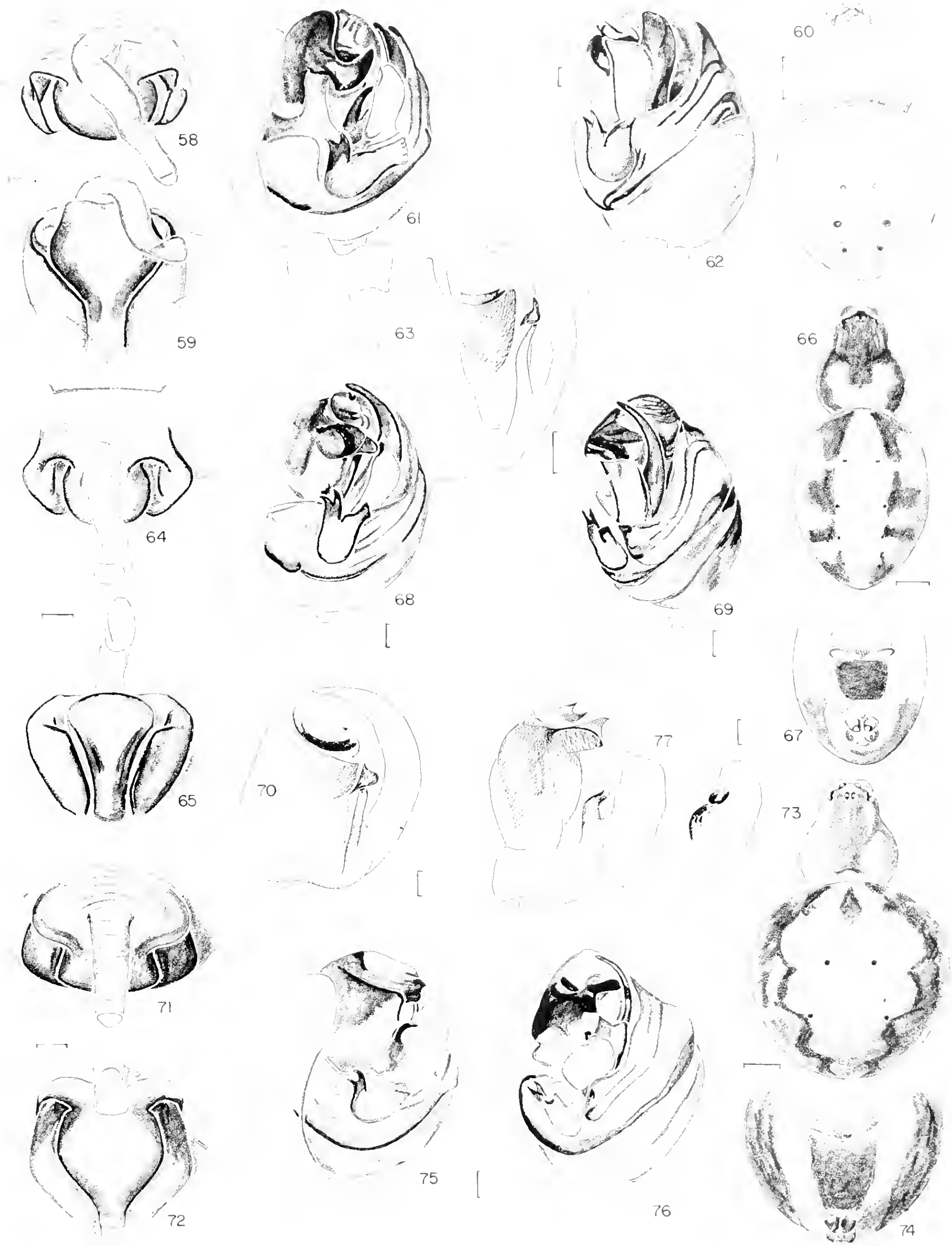
Figures 58–63. *Araneus unanimus* (Keyserling). 58–60. Female. 58. Epigynum, ventral. 59. Epigynum, posterior. 60. Dorsal. 61–63 Male, left palpus. 61. Mesal. 62. Ventral. 63. Embolus with cap, subterminal and terminal apophyses.

Figures 64–70. *A. vincibilis* (Keyserling). 64–67. Female. 64. Epigynum, ventral. 65. Epigynum, posterior. 66. Dorsal. 67. Abdomen, ventral. 68–70. Male. 68. Palpus, mesal. 69. Palpus, ventral. 70. Embolus with cap, subterminal and terminal apophyses.

Figures 71–77. *A. corporosus* (Keyserling). 71–74. Female. 71. Epigynum, ventral. 72. Epigynum, posterior. 73. Dorsal. 74. Abdomen, ventral. 75–77. Male. 75. Palpus, mesal. 76. Palpus, ventral. 77. Embolus without cap left, subterminal and terminal apophyses and with cap right.

Scale lines 1.0 mm, genitalia 0.1 mm.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Araneus vincibilis (Keyserling)
Plate 1; Figures 64–70; Map 2

Epeira vincibilis Keyserling, 1893: 2090, pl. 9, fig. 154. ♀. Female holotype from Rio Grande do Sul, Brazil, in BMNH, examined.
Aranea vincibilis:—Roewer, 1942: 856.
Aranea vincibilis:—Bonnet, 1955: 630.

Description. Female from São Paulo. Carapace dark brown with orange streak on each side of head and an orange U-shaped patch on thorax (Fig. 66). Labium and endites dark brown. Sternum dark brown with median white patch. Coxae orange; legs orange with dark brown rings. Dorsum of abdomen with median light band, pointed at each end, and dark patches on each side (Fig. 66); venter with square dark patch (Fig. 67). Posterior median eyes 0.7 diameter of anterior median eyes, lateral eyes 0.6 diameter. Anterior medians a little less than their diameter apart, their diameter from laterals. Posterior medians 0.6 diameter apart, 2 from laterals. Abdomen oval (Fig. 66). Total length 8.5 mm. Carapace 3.3 mm long, 2.8 wide. First femur 3.7 mm, patella and tibia 4.5, metatarsus 3.3, tarsus 1.2. Second patella and tibia 3.9 mm, third 2.3, fourth 3.5.

Male from Triunfo, Rio Grande do Sul. Carapace as in female, except head light with median brown patch; thorax as in female. Sternum light orange. Posterior median and lateral eyes 0.7 diameter of anterior medians. Anterior medians 0.4 diameter apart, 0.6 from laterals. Posterior medians 0.4 diameter apart, 1.5 from laterals. Endite with tooth. First coxa with hook. Abdomen oval. Second tibia thicker than first, with area of short macrosetae. Total length 5.8 mm. Carapace 3.1 mm long, 2.3 wide. First femur 3.8 mm, patella and tibia 4.6, metatarsus 3.4, tarsus 1.2. Second patella and tibia 3.2 mm, third 2.0, fourth 3.0.

Variation. Total length of females 7.2 to 9.9 mm, of males 4.4 to 5.8.

Diagnosis. All individuals, female and male, have a dark pattern on the thoracic part of the carapace (Fig. 66), although the head may be light. In ventral view, the epigynum (Fig. 64) resembles those of *A. omnicolor* (Fig. 49) and *A. unanimus*. In posterior view (Fig. 65) it has a ventrally round median plate (unlike the pentagonal plate of *A. unanimus*, Fig. 59) and lacks the median right-angled lobes of the lateral plates of *A. omnicolor* (Fig. 50).

The male has a distinctive median apophysis, its sides being almost parallel (Fig. 68), and a unique embolus cap that fits against the subterminal apophysis (Fig. 70). If the cap is missing (in mated individuals), the tip of the embolus is slightly bent toward the subterminal apophysis, away from the lamella and conductor.

Natural History. There is only one collection with both males and females. The consistent carapace pattern indicates that they belong together. There are more males than females in collections, suggesting that females may inhabit tree tops or some other place out of the reach of collectors.

Distribution. From Rio de Janeiro State, Brazil, to Caaguazú Department of Paraguay (Map 2).

Records. BRAZIL *Rio de Janeiro:* Serra dos Órgãos, 2000 m, ♂ (MCZ); Teresópolis, ♀ (AMNH); Rio de Janeiro, ♀ (AMNH); Tijuca, ♀ (MCZ). *São Paulo:* Jardim Botânico, São Paulo, ♀, ♂ (AMNH, MCZ, MZSP). *Paraná:* Curitiba, ♀ (MNRJ). *Rio Grande do Sul:* Triunfo, ♀, ♂ (MCN); Montenegro, ♂ (MCN); Garruchos, ♂ (MCN); Garruchos, Borja, ♂ (MCN); Canela, ♂ (MCN); Bom Jesus, ♂ (MCN); São Francisco de Paula, ♂ (MCN); Barra do Ribeiro, ♀ (MCN). PARAGUAY *Caaguazú:* Colónia Wolter Insfran, ♀ (IBNP). ARGENTINA *Misiones:* Eldorado, imm. ♂ (AMNH).

Araneus corporosus (Keyserling)
Figures 71–77; Map 2

Epeira corporosa Keyserling, 1892: 189, pl. 9, fig. 140, ♀. Female holotype from Taquara [Rio Grande do Sul], Brazil, in BMNH, examined.
Aranea corporosa:—Roewer, 1942: 840.
Metepeira delineata Mello-Leitão, 1943: 105, fig. 5, ♀. Female holotype from Cabaña [?], Córdoba, Ar-

gentina, in MLP, examined. Brignoli, 1983: 275. NEW SYNONYMY.

Eustala lactea Mello-Leitão, 1944: 329. Male holotype from Tigre, Buenos Aires Prov., Argentina, in MLP, examined. Brignoli, 1983: 269. NEW SYNONYMY.

Larinia nobilis Mello-Leitão, 1944: 331, fig. 15, ♂. Male holotype from Buenos Aires, Argentina, in MLP, examined. Brignoli, 1983: 272. NEW SYNONYMY.

Metepeira arabesca Mello-Leitão, 1947: 248, figs. 14, 15, ♀. Female holotype from Barigui, Mun. de Curitiba, Paraná, Brazil, in MHNC, examined. NEW SYNONYMY.

Araneus corporosus:—Bonnet, 1955: 470.

Description. Female from Campos do Jordão, São Paulo. Carapace orange, head darker with white setae. Chelicerae, labium, endites dark orange. Sternum light orange, darker anteriorly. Coxae orange; legs orange with darker rings. Dorsum of abdomen with dusky folium outline (Fig. 73); venter with black trapezoid and a light band on each side, dark to sides of bands (Fig. 74). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 1 diameter apart, 1 from laterals. Posterior median eyes 0.7 diameter apart, 2.4 from laterals. Abdomen spherical (Fig. 73). Total length 7.0 mm. Carapace 3.1 mm long, 2.4 wide. First femur 3.1 mm, patella and tibia 3.5, metatarsus 2.7, tarsus 1.0. Second patella and tibia 2.9 mm, third 1.9, fourth 2.7.

Male from Minas Gerais. Color as in female, but without rings on legs, and abdomen with only dorsal longitudinal white bands. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5. Anterior median eyes 1 diameter apart, 1.2 from laterals. Posterior median eyes 0.8 diameter apart, 2.2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first with some short macrosetae. Abdomen oval. Total length 5.6 mm. Carapace 3.0 mm long, 2.3 wide. First femur 3.8 mm, patella and tibia 4.6, metatarsus 3.3, tarsus 1.0. Second patella and tibia 3.5 mm, third 1.9, fourth 2.6.

Note. The male has not been collected with the female; this match is based on the male's similarity to the male of *A. workmani.*

Variation. Total length of females 5.2 to 8.3 mm, of males 4.2 to 4.3.

Diagnosis. Females are lighter in color than the similar *A. workmani.* As in *A. workmani*, but unlike other related species, *A. corporosus* has the median plate of the epigynum T-shaped in posterior view, but *A. corporosus* differs from *A. workmani* (Fig. 79) in having the median plate much wider than the lateral plates (Fig. 72). Males of *A. corporosus* (Fig. 76) and *A. workmani* (Fig. 83) differ from related species by having the embolus lamella with a shoulder (Figs. 76, 77); *A. corporosus* males differ from males of *A. workmani* (Fig. 82) and all similar species by having a bent embolus (Figs. 75, 77).

Distribution. From Minas Gerais, Brazil, to Buenos Aires Province, Argentina (Map 2).

Records. BRAZIL *Minas Gerais:* Lavras, ♂ (MCZ). *São Paulo:* Estr. Santos, Jurubatuba, ♀ (MZSP); Boruerú, ♀ (MZSP); São Paulo, ♀ (MZSP); Boqueri, ♀ (MZSP); Serra da Bocaina, ♂ (MZSP); Campos do Jordão, 2♀ (MZSP); Mogi das Cruzes, ♀ (MZSP); Itapeva, ♀ (MCZ). *Paraná:* Curitiba, ♀ (MNRJ, MZSP). *Santa Catarina:* Pinhal, ♀ (AMNH). *Rio Grande do Sul:* São Leopoldo, ♀ (MZSP); Esmeralda, ♀ (MCN); Santa Maria, ♀ (MCN); Montenegro, ♀ (MCN); Cambará do Sul, ♀ (MCN); Morro do Itacolomi Gravatai, ♀ (MCN). ARGENTINA *Salta:* 5 km S Jujuy, ♀ (MCZ). *Córdoba:* Valle Hermosa, ♀ (AMNH). *Buenos Aires:* Burzaco, ♀ (MACN); San Miguel, ♀ (MLP); José C. Paz, ♀ (MLP).

Araneus workmani (Keyserling)
Plate 1; Figures 78–84; Map 2

Epeira worckmanni Keyserling, 1884: 649, pl. 21, fig. 1, ♂. Male holotype from Santa Isabela, Rio Grande do Sul, Brazil, in NMI, examined.

Aranea worckmanni:—Roewer, 1942: 85.

Araneus workmani:—Bonnet, 1955: 632.

Note. Since the species was named after the arachnologist T. Workman of Dublin,

Bonnet emended the spelling. Dr. P. J. O'Sullivan, NMI (personal correspondence), wrote that the spelling by Bonnet is correct. Specimens in the BMNH labeled *Epeira workmanni* Keyserling [*sic*] are not the types and do not match Keyserling's illustrations. They are specimens of *Araneus uniformis.*

Description. Female from São Bernardo, São Paulo. Carapace dark brown with white setae. Chelicerae proximally orange, distally brown. Labium, endites brown. Sternum orange. Coxae orange; legs orange with dark brown rings. Dorsum of abdomen brown with paired light spots (Fig. 80); venter with two white bands on dark brown (Fig. 81). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.1 diameters apart, 1.2 from laterals. Posterior median eyes 0.9 diameter apart, 3.3 from laterals. Abdomen subspherical (Fig. 80). Total length 8.0 mm. Carapace 3.5 mm long, 3.1 wide. First femur 3.9 mm, patella and tibia 4.7, metatarsus 3.4, tarsus 1.2. Second patella and tibia 3.9 mm, third 2.5, fourth 3.5.

Male from São Bernardo, São Paulo. Color much lighter than that of female, mostly light orange. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart, 0.8 from laterals. Posterior median eyes 0.8 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first with some short macrosetae. Abdomen oval. Total length 6.0 mm. Carapace 3.2 mm long, 2.7 wide. First femur 4.2 mm, patella and tibia 5.1, metatarsus 3.4, tarsus 1.2. Second patella and tibia 3.9 mm, third 2.3, fourth 3.1.

Note. The first male encountered was collected with females of *A. stabilis,* but subsequently males were found with females here considered *A. workmani.*

Variation. Total length of females 6.4 to 10.0 mm, of males 5.2 to 6.1.

Diagnosis. Females are much darker in color than females of *A. corporosus.* As in *A. corporosus,* but unlike other related species, *A. workmani* has the median plate of the epigynum T-shaped in posterior view, but *A. workmani* differs from *A. corporosus* (Fig. 72) in having the median plate narrower than the lateral plates (Fig. 79). Males of *A. workmani* and *A. corporosus* differ from related species by having the embolus lamella with a shoulder (Figs. 82–84); *A. workmani* males differ from males of *A. corporosus* (Fig. 77) by having the embolus only slightly curved (Fig. 84).

Natural History. Females have been collected in bamboo undergrowths, on the roadside in a forest, and in a forest in Rio de Janeiro State.

Distribution. From Espírito Santo State, Brazil, to Buenos Aires Province, Argentina (Map 2).

Records. BRAZIL *Espírito Santo:* Morro Moscoso, Vitória, ♀ (MCN). *Rio de Janeiro:* Teresópolis, 1000 m, ♀ (AMNH); Alto da Tijuca, ♀ (MCZ); Pico da Tijuca, 500–950 m, ♀, ♂ (MCZ). *São Paulo:* São Paulo, ♀, ♂ (AMNH, MZSP, MCZ); Cocaia, Santo Amaro, ♀, ♂ (MZSP); São Bernardino, ♀, ♂ (MZSP); Boracéia, ♀, ♂ (MZSP); Campos do Jordão, ♀ (MZSP); Alto da Perdizes, ♀

→

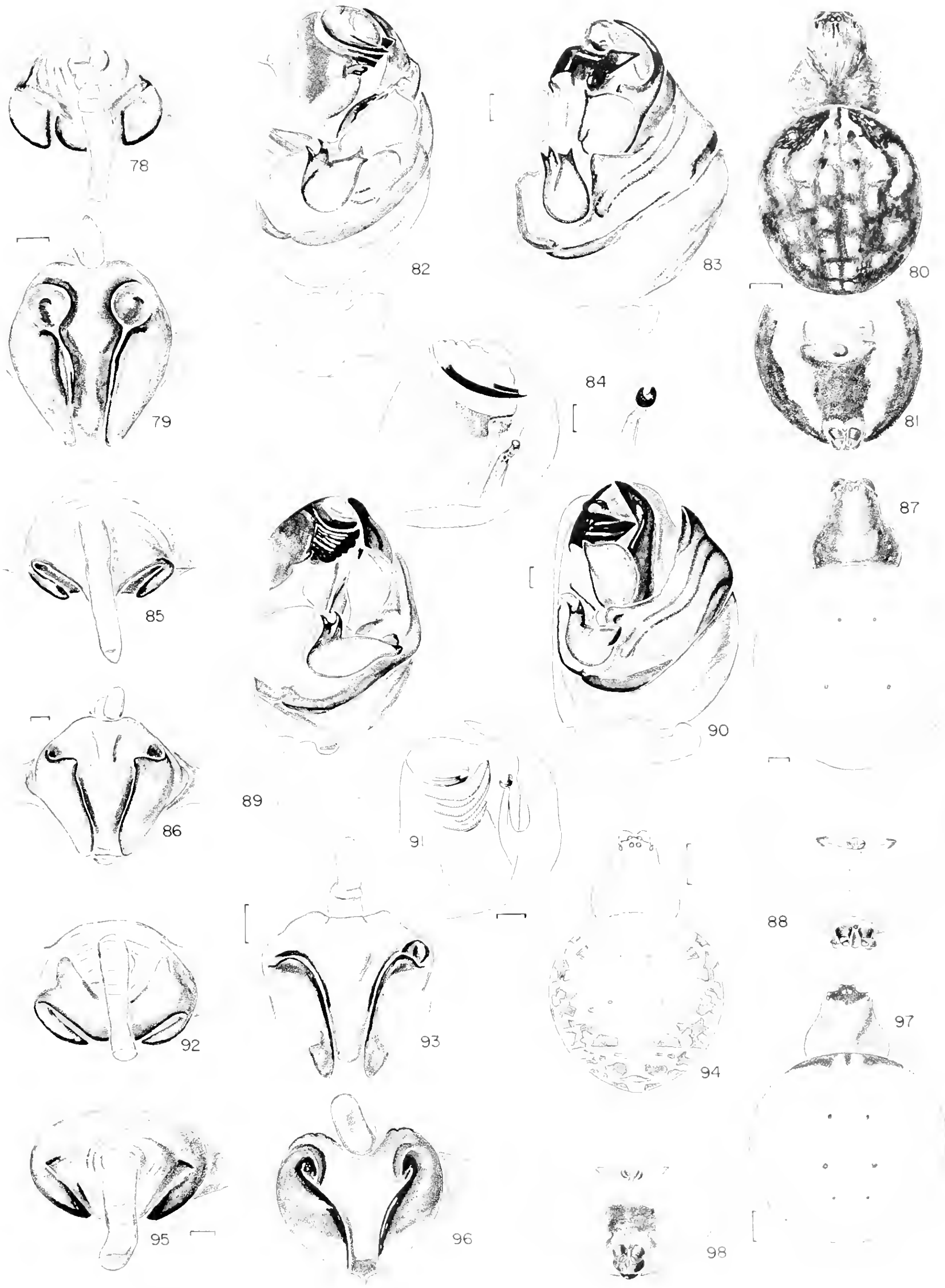
Figures 78–84. *Araneus workmani* (Keyserling). 78–81. Female. 78. Epigynum, ventral. 79. Epigynum, posterior. 80. Dorsal. 81. Abdomen, ventral. 82–84. Male, left palpus. 82. Mesal. 83. Ventral. 84. Embolus without cap, left, subterminal and terminal apophyses, and tip of embolus with cap, right.

Figures 85–91. *A. lathyrinus* (Holmberg). 85–88. Female. 85. Epigynum, ventral. 86. Epigynum, posterior. 87. Dorsal. 88. Abdomen, ventral. 89–91. Male palpus. 89. Mesal. 90. Ventral. 91. Embolus, subterminal and terminal apophyses.

Figures 92–94. *A. orgaos* n. sp., female. 92. Epigynum, ventral. 93. Epigynum, dorsal. 94. Dorsal.

Figures 95–98. *A. schneblei* n. sp., female. 95. Epigynum, ventral. 96. Epigynum, posterior. 97. Dorsal. 98. Abdomen, ventral.

... 1.0 mm, genitalia 0.1 mm.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MZSP); Cantareira, ♀ (MZSP); Salesópolis, ♀ (MZSP); Americana, ♀ (MZSP); Campos da Serra, ♀ (MZSP); Piracicaba, ♀ (MZSP); Serra Negra, ♀ (MZSP). *Paraná:* Antonina, ♂ (MNRJ). *Santa Catarina:* Pinhal, ♀ (AMNH); Morro dos Conventes, Araranguá, ♀ (MCN); Corupá, ♀ (AMNH). *Rio Grande do Sul:* Morro Teresópolis, Porto Alegre, ♀, ♂ (MCN); Vacaria, ♀ (MCN); Nova Petrópolis, ♂ (MCN); Pelotas, ♀ (MCN). ARGENTINA *Buenos Aires:* Florencia Varela, ♂ (MACN); Delta de Paraná, ♀, ♂ (MACN, MEG); Punta Lara, ♂ (MACN).

Araneus lathyrinus (Holmberg)
Figures 85–91; Map 2

Epeira lathyrina Holmberg, 1874a: 283, pl. 6, fig. 1. Specimens from Palermo, Belgrano, San Isidro, San Fernando, Las Conchas, Caballito, Flores, Chivilcoy, Navarro, Mercedes, Buenos Aires [all in Buenos Aires Prov.], Argentina, destroyed; 1874b: 95.

Epeira montevidensis Keyserling, 1878: 571, pl. 14, fig. 1, 2, ♀, ♂. Two female syntypes marked types, one male and one female with a Keyserling bordered label from Uruguay in BMNH, examined. Syntypes in Stuttgart Museum destroyed in World War II (Renner, 1988); 1892: 148, pl. 7, fig. 109, ♀, ♂.

Epeira caerulea Bertkau, 1880: 87, pl. 2, fig. 31, ♀. Four females from "Rio Grande" [?do Sul], lost. First synonymized by Keyserling, 1892.

Araneus lathyrinus:—Simon, 1897: 1. Synonymized *montevidensis* and *caerulea* with *lathyrina*.

Aranea lathyrina:—Roewer, 1942: 845.

Neoscona lathyrina:—Bonnet, 1958: 3061.

Description. Female from Rio Grande do Sul. Carapace dark brown on sides, midline orange, some white setae on sides of head. Chelicerae, labium, endites brown. Sternum, coxae orange; femora dark brown, indistinctly ringed; legs orange brown. Dorsum of abdomen whitish (Fig. 87); venter with a white square between epigastric groove and spinnerets overlain by brownish coloring (Fig. 88). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 1 diameter apart, 1.6 from laterals. Posterior median eyes 0.6 their diameter apart, 3.5 from laterals. Abdomen spherical (Fig. 87). Total length 13.7 mm. Carapace 4.9 mm long, 4.2 wide. First femur 4.5 mm, patella and tibia 5.9, metatarsus 4.5, tarsus 1.3. Second patella and tibia 4.9 mm, third 3.3, fourth 4.5.

Male from Rio Grande do Sul. Color as in female, except proximal ends of femora light, legs more distinctly ringed and a black band around anterior of abdomen. Posterior median eyes 0.6 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.6 diameter apart, 3 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with macrosetae. Abdomen oval. Total length 8.6 mm. Carapace 4.7 mm long, 3.6 wide. First femur 6.9 mm, patella and tibia 7.9, metatarsus 6.9, tarsus 1.3. Second patella and tibia 5.9 mm, third 3.1, fourth 4.5.

Variation. Total length of females 6.2 to 14 mm, of males 6.4 to 7.4. Freshly preserved specimens are green in color. The carapace is sometimes light, sometimes with two dark bands, one on each side of the thorax.

Diagnosis. The female differs from females of similar species without an abdominal pattern by having the epigynum in ventral view with diagonal slits far posterior (Fig. 85). In posterior view the lateral plates have a lobe on each side toward the median as does *A. omnicolor* (Fig. 50), but the median plate has a pair of distinct, ventral, shallow depressions (Fig. 86) not present in *A. orgaos* (Fig. 93), *A. omnicolor* (Fig. 50), or *A. unanimus* (Fig. 59).

The male differs from males of similar species in that the tip of the embolus approaches a lobe of the lamella (Fig. 91) and the subterminal apophysis has a series of ridges separated by grooves (Figs. 89, 91).

Note. The first right leg of a male is regenerated and much shorter.

Natural History. The egg-sac collected with a female is a woolly sphere the size of the female abdomen and is secured within a curled leaf.

Distribution. From Rio de Janeiro State, Brazil, to Buenos Aires Province, Argentina (Map 2).

Records. BRAZIL *Santa Catarina:* Pinhal, ♀ (AMNH). *Rio Grande do Sul:* São Leopoldo, ♀, ♂ (MZSP); Est. Ecologica do Taim, ♀, ♂ (MCN); Montenegro, ♀, ♂ (MCN); Dona Francisca, ♀ (MCN); São Sepé, ♀ (MCN); Bagé, ♀ (MCN); Bom Jesus, ♂ (MCN); Itaimbezinho, Cambará do Sul, ♂ (MCN); Est. Ecológ. do Aracun Esmeralda, ♀ (MCN); Canela, ♀ (MCN); Pelotas, ♀ (MCN, AMNH). PARAGUAY *Alto Paraná:* Hernandarías, ♂ (MCZ). *Itapúa:* Capitán Meza, ♀ (IBNP). ARGENTINA *Misiones:* Candelaria, 2♀ (MACN); San Pedro, ♀ (MACN); Eldorado, ♂ (AMNH). *Córdoba:* Calamuchita, ♀ (MACN). *San Luis:* Merlo, ♀ (MACN); Villa Elena, ♀ (MACN). *Buenos Aires:* Moreno, ♀ (MACN); Zelaya, ♀ (MACN).

Araneus orgaos new species
Figures 92–94; Map 2

Holotype. Female holotype and female paratype from Serra dos Órgãos, 1000–1500 m, forest, Est. Rio de Janeiro, Brazil, 20 Apr. 1965 (H. Levi), in MZSP, ex MCZ. The specific name is a noun in apposition after the type locality, the Portuguese word for organ.

Description. Female holotype. Carapace, sternum orange. Legs orange, fourth tibia, metatarsus, tarsus with distal black rings. Paired dusky marks on sides and posterior of dorsum of abdomen (Fig. 94). Venter with white pigment spots and some dusky pigment in center between epigynum and spinnerets. Posterior median eyes same diameter as anterior median eyes, lateral eyes 0.8 diameter. Anterior median eyes their diameter apart, a little more than their diameter from laterals. Posterior median eyes 0.6 diameter apart, 2 from laterals. Abdomen spherical. Total length 6.4 mm. Carapace 2.7 mm long, 2.3 wide. First femur 3.1 mm, patella and tibia 3.7, metatarsus 2.3, tarsus 0.9. Second patella and tibia 3.0 mm, third 1.8, fourth 2.6.

Variation. The lateral plates of the epigynum in some specimens are farther apart than in the specimen illustrated.

Diagnosis. This species differs from *A. lathyrinus* (Fig. 86) in lacking the pair of ventral depressions on the posterior median plate of the epigynum (Fig. 93) and from *A. blumenau* (Fig. 43) by the triangular shape of the posterior median plate (Fig. 93).

Paratypes. BRAZIL *Est. Rio de Janeiro:* Serra dos Órgãos, 19 Apr. 1965, 2♀ (H. Levi, MCZ). *São Paulo:* Mata do Governor, Inst. Botânico, 4 Mar. 1959, ♀ (L. Lane, AMNH).

Araneus schneblei new species
Figures 95–98; Map 2

Holotype. Female from Medellín, Antioquia, Colombia, Jan., Feb. 1963 (P. B. Schneble), in MCZ. The species is named after the collector.

Description. Female. Carapace orange, eye region black. Sternum and legs orange. Dorsum of abdomen with tiny white spots, black anteriorly on sides (Fig. 97). Venter with a median black band, spinnerets black (Fig. 98). Carapace without setae. Eyes subequal. Anterior median eyes their diameter apart, 1.7 from laterals. Posterior median eyes 0.6 diameter apart, 3 from laterals. Abdomen spherical. Total length 9.0 mm. Carapace 4.2 mm long, 3.5 wide. First femur 4.4 mm, patella and tibia 5.1, metatarsus 3.7, tarsus 1.1. Second patella and tibia 4.6 mm, third 2.7, fourth 4.0.

Diagnosis. In posterior view of the epigynum of *A. schneblei*, the median edge of the lateral plates curls anteriorly (Fig. 96) while that of the Brazilian *A. orgaos* (Fig. 93) curves laterally. The median plate lacks the depressions present in *A. lathyrinus* (Fig. 86) of southeastern South America.

Araneus horizonte new species
Figures 99–104; Map 2

Holotype. Female holotype from Belo Horizonte, Minas Gerais, Brazil (C. Mello-Leitão), in MNRJ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange with median dark brown band. Chelicerae, labium, endites orange. Sternum orange underlain by white pigment in middle. Coxae orange; legs orange with brown rings. Dorsum of abdomen white with a pair of anterior black marks (Fig. 103); venter with a black patch of indistinct outline (Fig. 104). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 0.9 diameter apart, 1.2 from laterals. Posterior median eyes 0.3 their diameter apart, 3 from laterals. Abdomen spherical (Fig. 103). Total length 12.7 mm. Carapace 5.2 mm long, 4.5 wide. First femur 5.2 mm, patella and tibia 6.4, metatarsus 4.9, tarsus 1.8. Second patella and tibia 5.7 mm, third 3.5, fourth 5.4.

Variation. Total length of females 8.6 to 12.7 mm. The extent of the dark marks on the carapace is variable. In the epigynum, the characteristic ventral holes in posterior view are elongate in the specimen from Peru, round in the specimens from Minas Gerais. The posterior median plate is longer in the Peruvian female (Fig. 102) than in the Minas Gerais female (Fig. 100).

Diagnosis. Araneus horizonte is larger than *A. corporosus*, and the epigynum differs in posterior view by having depressions framed by sclerotized rims and by the median plate being pentagonal (Figs. 100, 102). It is very similar to *A. taperae* (Fig. 106), but is distinguished by a narrower posterior median plate (Figs. 100, 102).

Distribution. From Amazon area of Colombia to Minas Gerais, Brazil, and Paraguay (Map 2).

Paratypes. COLOMBIA *Amazonas:* Leticia, 16 June 1965, ♀ (P. R. Craig, J. Robb, DU). ECUADOR *Napo:* Cuyabeno, Lago Agrio Airport, 10 Aug. 1988 (W. Maddison, MCZ). PERU *Huánuco:* Tingo María, Dec. 1946, ♀ (W. Weyrauch, AMNH). *Cusco:* Quillabamba, 7 July 1987, ♀ (MHNSM). BRAZIL *Pará:* Boa Vista, 18 Sept. 1964, ♀ (J. Olazarri, CAS). PARAGUAY *Cordillera:* Instit. Agric. Nac. Caocupé, 28 Mar. 1981, ♀ (R. D. Cave, IBNP).

Araneus taperae (Mello-Leitão) new combination
Figures 105–108; Map 2

Metepeira taperae Mello-Leitão, 1937: 7, fig. 9, ♀. Female holotype from Tapera, Pernambuco, Brazil, in MNRJ, examined. Roewer, 1942: 868.

Metepeira taperana:—Bonnet, 1957: 2823. An invalid name change.

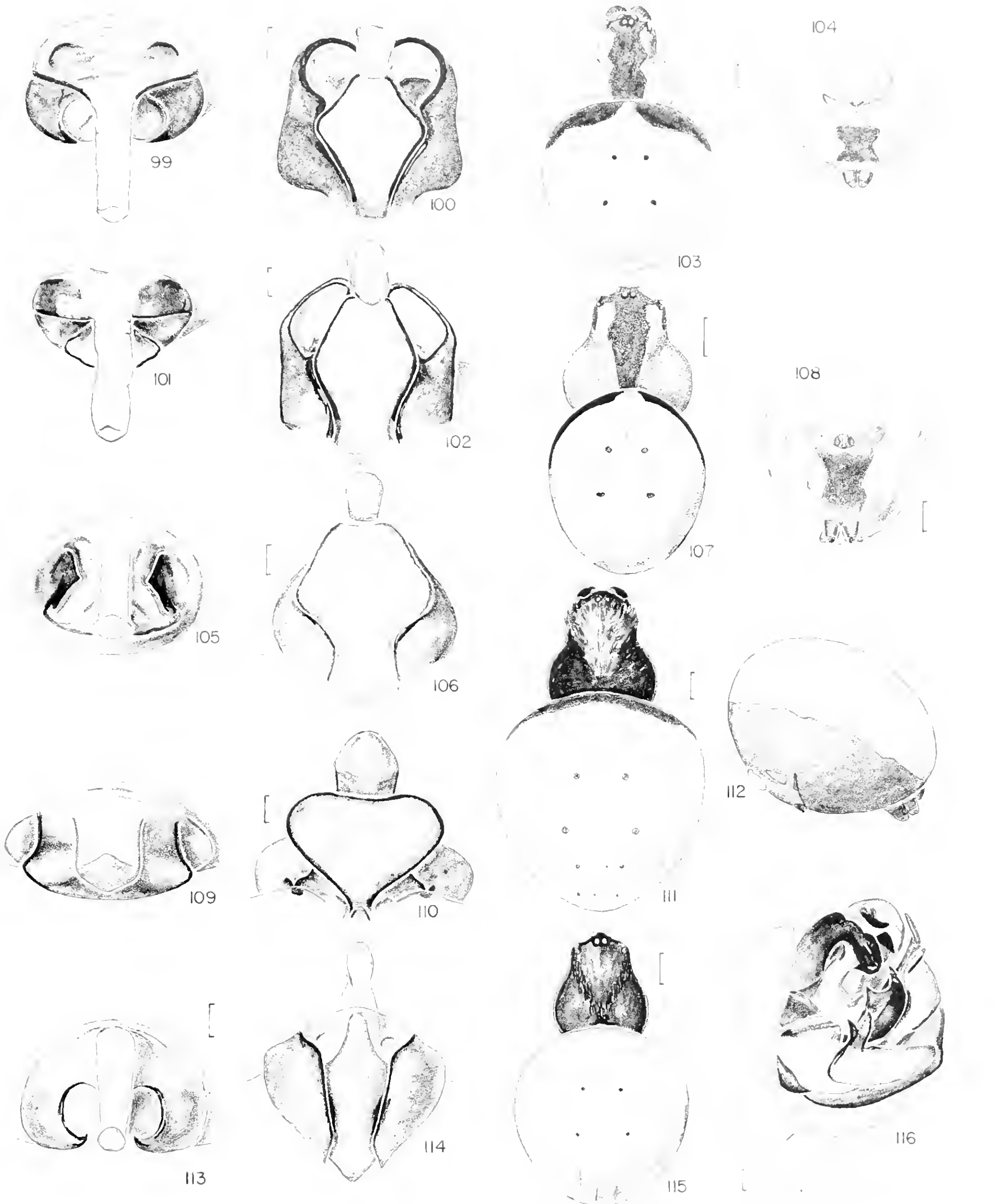
Description. Female from Surinam. Carapace orange, head darker orange-brown. Chelicerae brown. Labium, endites light orange. Sternum orange underlain by white pigment in center. Coxae orange; legs indistinctly ringed orange-brown on orange. Dorsum of abdomen white with transverse bars posteriorly on sides (Fig. 107); venter with paired white patches, black between, spinnerets orange-brown (Fig. 108). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 1 diameter apart, 1.6 from laterals. Posterior median eyes 0.5 diameter apart, slightly more than 3 from laterals. Abdomen with humps, almost shield-shaped (Fig. 107). Total length 10.5 mm. Carapace 4.9 mm long, 4.2 wide. First femur 5.4 mm, patella and tibia 6.6, metatarsus 4.9, tarsus 1.9. Second patella and tibia 6.0 mm, third 3.7, fourth 5.5.

Variation. Total length of females 10.1 to 12.3 mm. The holotype has a spherical abdomen and dorsal marks as in *A. horizonte* (Fig. 103). The abdomen of the specimen from Manaus is dark.

Diagnosis. This species differs from the similar *A. horizonte* (Figs. 100, 102) by having a wider posterior median plate of the epigynum; the depressions on each side, visible in ventral view (Fig. 105), are hidden in posterior view (Fig. 106).

Distribution. From Surinam to Amazonian Ecuador (Map 2).

Records. SURINAM ♀ (C. J. Herring, USNM); Jagtlust, June 1938, ♀ (Geiskes, AMNH). ECUADOR *Napo:* Río Tarapuy, 18 Nov. 1982, ♀ (L. Avilés, MECN). BRAZIL *Amazonas:* Manaus, Tarumã Mirím,



Figures 99–104. *Araneus horizonte* n. sp., female. 99, 101. Epigynum, ventral. 100, 102. Epigynum, posterior. 103. Dorsal. 104. Abdomen, ventral. 99, 100, 103, 104 (Minas Gerais, Brazil). 101, 102 (Peru).

Figures 105–108. *A. taperae* (Mello-Leitão), female. 105. Epigynum, ventral. 106. Epigynum, posterior. 107. Dorsal. 108. Abdomen, ventral.

Figures 109–112. *A. sernai* n. sp., female. 109. Epigynum, ventral. 110. Epigynum, posterior. 111. Dorsal. 112. Abdomen, lateral.

Figures 113–115. *A. bandelieri* Simon, female. 113. Epigynum, ventral. 114. Epigynum, posterior. 115. Dorsal.

Figure 116. *A. xavantina* n. sp., male, left palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

flooded forest, 13 May 1983, ♀ (J. Adis, M. Höfer, INPA). *Pará:* Tucuriú, Jan. 1979, ♀ (L. C. F. Alvarenga, MNRJ). *Pernambuco:* Tapera, ♀ (B. Pickel, MNRJ).

Araneus sernai new species
Figures 109–112; Map 2

Holotype. Female holotype, two female paratypes and one immature from San Pedro, Dpto. Antioquia, Colombia, 12 July 1986 (M. A. Serna), in MCZ. The species is named after the collector.

Description. Female. Carapace dark brown with white setae. Chelicerae, labium, endites, sternum, coxae, legs dark brown. Dorsum of abdomen orange-white, venter black (Figs. 111, 112). Secondary eyes 0.6 diameter of anterior medians. Anterior median eyes 1 diameter apart, 1.8 from laterals. Posterior median eyes 0.8 diameter apart, 4.5 from laterals. Abdomen spherical. Total length 12.0 mm. Carapace 5.2 mm long, 4.1 wide. First femur 3.9 mm, patella and tibia 4.8, metatarsus 3.1, tarsus 1.3. Second patella and tibia 4.2 mm, third 2.7, fourth 4.0.

Variation. Total length 11.0 to 12.0 mm.

Diagnosis. The female is distinguished by the very short scape sitting on a ventral projection formed by the bulging posterior median plate of the epigynum (Figs. 109, 110).

Natural History. Specimens were collected in an orange orchard in *Tibouchina* shrubs (Melastomataceae), 3 km from San Pedro at an altitude of 2500 m.

Paratype. COLOMBIA *Boyacá:* Río Upía, 850–950 m, Nov., Dec. 1945, ♀ (AMNH).

Araneus bandelieri (Simon)
Figures 113–115; Map 2

Epeira bandelieri Simon, 1891: 10. Female holotype from Tovar [Mérida], Venezuela, in MNHN, examined.

Aranea bandelieri:—Roewer, 1942: 837.

Araneus bandelieri:—Bonnet, 1955: 441.

Description. Female from Caracas. Carapace dark brown with white setae. Chelicerae, labium, endites dark brown. Sternum dark brown, lighter in a median longitudinal line. Coxae, legs dark brown. Dorsum of abdomen whitish (Fig. 115); venter with transverse dusky patch behind genital groove, followed by an equal-sized white area. Posterior median and lateral eyes 0.8 diameter of anterior medians. Anterior median eyes 1.3 diameters apart, 2 from laterals. Posterior median eyes 0.8 their diameter apart, 3.3 from laterals. Abdomen spherical (Fig. 115). Total length 9.0 mm. Carapace 4.2 mm long, 3.5 wide. First femur 4.2 mm, patella and tibia 4.4, metatarsus 3.8, tarsus 1.4. Second patella and tibia 4.3 mm, third 2.7, fourth 3.9.

Variation. Total length of females 8.7 to 11.0 mm. The holotype specimen has the epigynum lightly sclerotized, the scape has parallel sides, and the two depressions are slightly smaller in size than those of the illustrated specimen from Caracas.

Diagnosis. Unlike other Neotropical *Araneus* species, *A. bandelieri* has the scape flanked by a pair of oval bordered depressions (Fig. 113); in posterior view the paired depressions flank a median ventral extension of the median plate (Fig. 114).

Natural History. According to Simon (1891), this species is social and many females place their egg-sacs in one large common silken sac. None of the recent collections records the species as being social.

Distribution. Venezuela, Brazil (Map 2).

Records. VENEZUELA *Distrito Federal:* San José del Avila, Caracas, 1940, ♀ (P. C. Vogl, AMNH); Caracas, Feb. 1927, ♀ (M. Pittier, USNM). BRAZIL *Minas Gerais:* Minas Serinha, Diamantina, Jan.–Mar. 1945, 2♀ (E. Cohn, AMNH). *São Paulo:* São Paulo, June 1967, ♀ (L. T. Filho, MZSP 6573). *Paraná:* Curitiba, ♀ (F. Lange, MNRJ). *Rio Grande do Sul:* Canela, 11 Jan. 1966, ♀ (A. A. Lise, MCN 0693).

Araneus xavantina new species
Figure 116; Map 2

Holotype. Male holotype from 260 km N of Xavantina, Est. Mato Grosso, 12°49′S, 51°46′W, 400 m el., Brazil, Feb.–Apr. 1969, in cerrado scrub (Xavantina–Cachimbo Exped.), MZSP, ex MCZ. The

specific name is a noun in apposition after the type locality.

Description. Male. Carapace dark orange to brown in eye region. Chelicerae brown. Labium, endites orange. Sternum orange with dark margin. Coxae orange-gray; legs dark orange (mostly broken off). Dorsum of abdomen with a black band around anterior, widened toward dorsum on each side and in middle, white behind; indistinct pairs of black bars on gray posteriorly; venter with white transverse pigment behind genital groove; a black transverse rectangle behind, surrounded by white pigment spots. Posterior median eyes same diameter as anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes slightly less than their diameter apart, 0.8 from laterals. Posterior median eyes 0.5 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Abdomen oval, pointed behind. Total length 5.8 mm. Carapace 2.8 mm long, 2.5 wide. First femur 3.7 mm. Fourth patella and tibia 2.8 mm.

Diagnosis. This species is distinguished from others by the bulky round embolus, whose lateral edge touches the conductor (Fig. 116), and by the long median apophysis.

Araneus pico new species
Figures 117–121; Map 2

Holotype. Female holotype from Pico da Tijuca, 500–950 m, Est. Rio de Janeiro, Brazil, 17 Apr. 1965 (H. Levi), in MZSP, ex MCZ. The specific name is a noun in apposition after the geographical feature.

Description. Female. Carapace dark orange-brown with white setae. Chelicerae dark brown. Labium, endites light with dark brown. Sternum light orange with sides brown. Coxae light orange; legs light orange, ringed orange-brown. Dorsum of abdomen with black and white pattern (Fig. 119); venter with median black square on gray (Fig. 120). Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes slightly less than 1 diameter apart, 1.5 from laterals. Posterior median eyes 0.5 diameter apart, 2.2 from laterals. Abdomen oval, longer than wide (Fig. 119). Total length 8.5 mm. Carapace 3.6 mm long, 3.1 wide. First femur 4.5 mm, patella and tibia 5.5, metatarsus 4.4, tarsus 1.2. Second patella and tibia 4.7 mm, third 2.9, fourth 4.0.

Male. Coloration as in female. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes slightly less than 1 diameter apart, 1 from laterals. Posterior median eyes 0.5 diameter apart, 2.3 from laterals. Endite without tooth. First coxa with hook. Second tibia slightly thicker than first. Abdomen oval. Total length 7.0 mm. Carapace 3.5 mm long, 2.9 wide. First femur 5.8 mm, patella and tibia 7.1, metatarsus 6.2, tarsus 1.5. Second patella and tibia 5.6 mm, third 2.8, fourth 4.0.

Variation. Total length of females 8.5 to 10.3 mm.

Diagnosis. Females differ from others by the short scape (Fig. 117) and large heart-shaped posterior median plate of the epigynum; also, the epigynum is smooth (Fig. 118), unlike the epigyna of *A. carchi* (Fig. 123) and *A. penai* (Fig. 129). Males have a large curved terminal apophysis in the palpus (Fig. 121), and the median apophysis is higher than long (Fig. 121).

Paratypes. BRAZIL *Rio de Janeiro:* Teresópolis, 900–1000 m, Mar. 1946, 2♀ (H. Sick, AMNH); Rio de Janeiro, 200–400 m, Jan., Feb. 1948, ♀ (H. Sick, AMNH). *Paraná:* Cavinna [?], 1947, ♀ (A. Maller, AMNH).

Araneus carchi new species
Figures 122–127; Map 2

Holotype. Female holotype with male paratype from Troya, 2900–2950 m, Carchi Prov., Ecuador, 13 June 1965 (L. Peña), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace dark orange, sides of head and thorax darker. The posterior median eyes have oval black rings which almost meet. Labium brown; endites orange. Sternum dark

brown. Coxae and legs orange. Dorsum of abdomen with two pairs of white patches framed by black (Fig. 124); venter dark orange-gray with two longitudinal white lines (Fig. 125). Eyes subequal. Anterior medians 1.3 their diameter apart, 1.3 from laterals. Posterior medians their diameter apart, 2.5 from laterals. Abdomen oval. Total length 5.0 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.1 mm, patella and tibia 2.5, metatarsus 1.6, tarsus 0.8. Second patella and tibia 2.1 mm, third 1.5, fourth 2.0.

Male. Color as in female, but without dorsal white patches on abdomen. Dorsum of abdomen lighter on sides than in middle. Thoracic depression an indistinct line. Eyes subequal. Anterior median eyes 1.7 their diameter apart, 1.5 from lateral. Posterior medians a little less than their diameter apart, 2.5 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with macrosetae. Abdomen wider than long. Total length 4.4 mm. Carapace 2.5 mm long, 2.1 wide. First femur 2.5 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.9. Second patella and tibia 2.1 mm; third 1.5, fourth 1.9.

Variation. Total length of females 5.0 to 5.7 mm, of males 4.0 to 4.7. The four white patches on the abdomen of the holotype are not present in all specimens.

Diagnosis. The female differs from that of *A. penai* (Fig. 128) by having a longer scape (Fig. 122) and a narrower posterior median plate of the epigynum (Fig. 123). The male differs from that of *A. penai* (Fig. 121) by having a U-shaped median apophysis (Fig. 126) and a differently shaped embolus lamella (Fig. 127).

Distribution. Ecuadorian Andes, 2600–3300 m (Map 2).

Paratypes. ECUADOR *Carchi:* Troya, 2900 m, 10–13 June 1965, ♀ (L. Peña, MCZ). *Imbabura:* Cuicocha, 27 May 1939, ♀ (F. M. Brown, AMNH). *Pichincha:* 3 km S Chillogallo, 3300 m, 17 Jan. 1974, ♀, ♂ (R. M. King, CAS); Quito, 21 Dec. 1958, ♂ (A. M. Nadler, AMNH); Panecillo nr. Quito, 25 Mar. 1880, ♂ (BMNH). *Tungurahua:* Tungurahua, 2600 m, 6 May 1939, 2♀, 2♂ (W. M. Clarke Macintyre, AMNH). *Bolívar:* Hda. Talahua, 3100 m, 29 Apr. 1939, ♂ (F. M. Brown, AMNH).

Araneus penai new species
Figures 128–132; Map 2

Holotype. Female holotype and two male paratypes from km 52, S of Cuenca, 3200 m, Azuay, Ecuador, 21 Mar. 1965 (L. Peña), in MCZ. The species is named after the collector.

Description. Female holotype. Carapace orange with dusky marks on sides. Chelicerae orange. Labium, endites brown. Sternum dark brown. Coxae light orange. Legs orange with indistinct darker rings. Dorsum of abdomen with three light bands, darker and mottled between two outer bands (Fig. 130); venter dark between epigynum and spinnerets, a light band on each side. Eyes subequal. Anterior median eyes 1.4 diameters apart, 1.5 from laterals. Posterior median eyes 0.8 their diameter apart, slightly more than 2 from laterals. Abdomen oval, widest in middle (Fig. 130).

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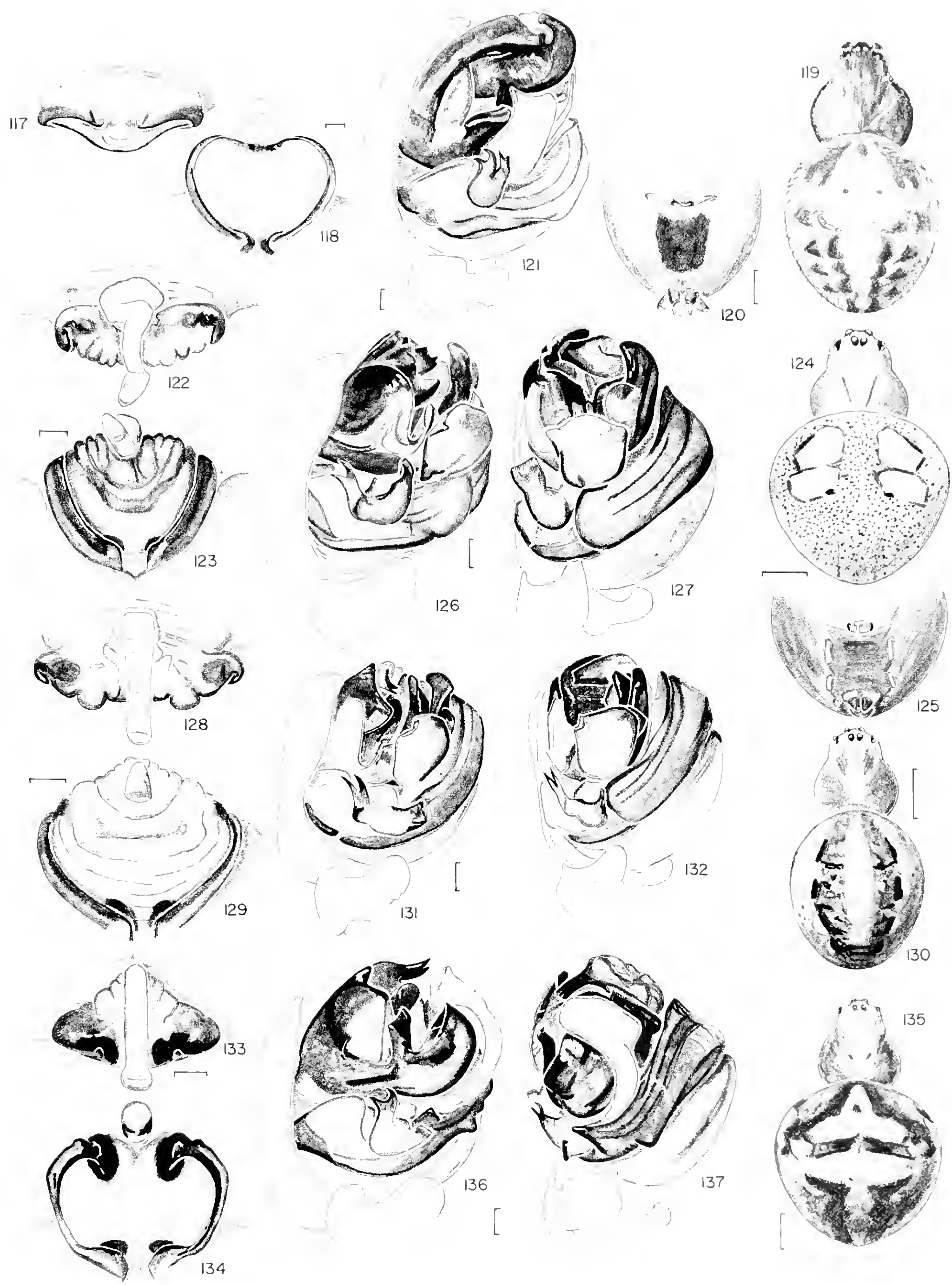
Figures 117–121. *Araneus pico* n. sp. 117–120. Female. 117. Epigynum, ventral. 118. Epigynum, posterior. 119. Dorsal. 120. Abdomen, ventral. 121. Male, left palpus.

Figures 122–127. *A. carchi* n. sp. 122–125. Female. 122. Epigynum, ventral. 123. Epigynum, posterior. 124. Dorsal. 125. Abdomen, ventral. 126. Male palpus, mesal. 127. Palpus, ventral.

Figures 128–132. *A. penai* n. sp. 128–130. Female. 128. Epigynum, ventral. 129. Epigynum, posterior. 130. Dorsal. 131. Male palpus, mesal. 132. Palpus, ventral.

Figures 133–137. *A. urubamba* n. sp. 133–135. Female. 133. Epigynum, ventral. 134. Epigynum, posterior. 135. Dorsal. 136. Male palpus, mesal. 137. Palpus, ventral.

[illegible] 1.0 mm, genitalia 0.1 mm.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Total length 4.7 mm. Carapace 2.1 mm long, 1.7 wide. First femur 1.8 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.9 mm, third 1.3, fourth 1.7.

Male. Coloration as in female except carapace all orange and abdomen less spotted. Thoracic depression with line. Eyes subequal. Anterior median eyes 1.2 diameters apart, 1.2 from laterals. Posterior median eyes slightly less than their diameter apart, 2 from laterals. Endite with large pointed tooth. First coxa with hook. Second tibia thicker than first, with short macrosetae. Abdomen oval. Total length 4.6 mm. Carapace 2.2 mm long, 1.9 wide. First femur 2.2 mm, patella and tibia 2.7, metatarsus 1.6, tarsus 0.7. Second patella and tibia 2.0 mm, third 1.3, fourth 1.7.

Note. The abdomen of the female holotype is damaged at its anterior end and the specimen has a regenerated left second leg.

Variation. A second female has a wider abdomen than the holotype.

Diagnosis. Females have a shorter scape (Fig. 128) than *A. carchi* (Fig. 122) and a wider posterior median plate in the epigynum (Fig. 129). Males have the median apophysis only slightly curved (Fig. 131) and the embolar lamella of a different shape (Fig. 132).

Distribution. Ecuador, at high elevations (Map 2).

Record. ECUADOR *Pichincha:* Hacienda Guachalá nr. Cayambe, ♀ (BMNH). *Azuay:* Lagunas de Cajas Bosque Migui, 2°50′S, 79°15′W, 20 Aug. 1988, ♀ (W. Maddison, MECN).

Araneus urubamba new species
Plate 1; Figures 133–137; Map 2

Holotype. Male holotype and three female paratypes from Urubamba, 2800 m, arid shrubs, stones, Dpto. Cusco, Peru, 18 Feb. 1965 (H. Levi), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, head orange, sides of thorax dusky brown with white down. Chelicerae, labium, endites brown. Sternum brown with median longitudinal white marks. Coxae orange; legs orange with indistinct narrow dusky rings. Dorsum of abdomen with two pairs of light patches and a transverse dark band between first and second pair (Fig. 135); venter with a dusky brown band between epigynum and spinnerets. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.8 diameters apart, 2.5 from laterals. Posterior median eyes 1.2 their diameter apart, 3.7 from laterals. Abdomen subspherical, widest anteriorly. Total length 6.5 mm. Carapace 2.7 mm long, 2.0 wide. First femur 2.8 mm, patella and tibia 3.4, metatarsus 2.2, tarsus 0.8. Second patella and tibia 2.7 mm, third 1.6, fourth 2.3.

Male. Coloration as in female except abdomen with white cardiac mark and mottling on dorsum. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.5 their diameter apart, 1.5 from laterals. Posterior median eyes 1.2 their diameter apart, 2.5 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with macrosetae. Abdomen oval. Total length 4.9 mm. Carapace 2.5 mm long, 2.2 wide. First femur 3.6 mm, patella and tibia 4.5, metatarsus 3.1, tarsus 1.1. Second patella and tibia 2.9 mm, third 1.7, fourth 2.5.

Variation. The photograph of a living female (Plate 1) shows the female to be shades of brown. Total length of females 6.2 to 6.8 mm, of males 4.2 to 4.9. In females, the dorsal pattern of the abdomen is variable.

Diagnosis. The female of *A. urubamba* differs from both *A. penai* (Fig. 128) and *A. carchi* (Fig. 122) in having the posterior edge of the base of the epigynum sclerotized (Fig. 133). In posterior view, the median plate has transverse wrinkles, as in *A. penai* (Fig. 129) and *A. carchi* (Fig. 123), but in *A. urubamba* the median plate is bordered ventrally by lateral plates (Fig. 134). The scape is narrower than that of

A. acolla (Fig. 138) and the base lacks the lobed appearance (Fig. 133) of *A. acolla* (Fig. 138). The male has a very distinct, large, sclerotized embolus and a stalked conductor (Figs. 136, 137).

Natural History. The female from the Tarma valley was collected at a rock outcrop.

Distribution. Peruvian mountains (Map 2).

Paratypes. PERU *Junín:* Cochas Bajo, Tarma Valley, 3600 m, 27 Mar. 1988, ♀ (J. Palmer, D. Smith, MCZ). *Cusco:* Cusco, 3600 m, 25 Feb. 1947, ♀, 2♂ (J. C. Pallister, AMNH); Hacienda Ocapana Ocongate, 3350 m, 6–11 Apr. 1947, 3♀, 2♂ (J. C. Pallister, AMNH).

Araneus acolla new species
Figures 138–141; Map 2

Holotype. Female holotype from Acolla, Dpto. Junín, 3460 m, Peru, 13 Sept. 1955 (F. Blancas), in MHNSM. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace dark orange-brown with white down; sides of thorax black. Chelicerae dark orange. Labium, endites dark brown. Sternum dark brown. Coxae light brown; legs dark orange. Dorsum of abdomen brown and white with paired black patches (Fig. 140); venter with dark brown band between epigynum and spinnerets (Fig. 141). Posterior median eyes same diameter as anterior medians, anterior laterals 0.9 diameter, posterior laterals 0.8. Anterior median eyes 1.2 diameters apart, 2 from laterals. Posterior median eyes slightly more than their diameter apart, 2.8 from laterals. Abdomen oval, longer than wide (that of type specimen shrivelled). Total length 7.0 mm. Carapace 3.4 mm long, 2.7 wide. First femur 3.1 mm, patella and tibia 3.8, metatarsus 2.6, tarsus 1.1. Second patella and tibia 3.1 mm, third 1.8, fourth 2.8.

Diagnosis. Araneus acolla differs from *A. urubamba* (Fig. 133, 134) by having a wider scape, a lobed base of the epigynum in ventral view (Fig. 138), and by having the lateral plates wider in posterior view (Fig. 139).

Araneus moretonae new species
Figures 142–145; Map 2

Holotype. Female holotype and two immature paratypes from Machupicchu, between hotel and station, Dpto. Cusco, Peru, 26 Jan. 1973 (A. Moreton), in MCZ. The species is named after Ann Moreton, the collector, who interested many young people in spiders.

Description. Female. Carapace red-brown. Chelicerae, labium, endites, sternum dark brown. Coxae orange. Legs orange with brown rings. Dorsum of abdomen with two white patches and symmetrical dark brown markings on lighter brown (Fig. 144); venter brown with a lighter brown longitudinal band on each side and streaked on sides of band (Fig. 145). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 1.2 diameters apart, 1.8 from laterals. Posterior median eyes 0.7 their diameter apart, 3.7 from laterals. Abdomen subspherical, dorsoventrally slightly flattened. Total length 9.2 mm. Carapace 4.4 mm long, 3.6 wide. First femur 4.4 mm, patella and tibia 5.4, metatarsus 3.9, tarsus 1.5. Second patella and tibia 4.7 mm, third 2.9, fourth 4.1.

Variation. The Cusco paratypes lack the two white patches on the dorsum and also have fewer dark marks on the dorsum of the abdomen, most dark marks being on the sides. In the paratypes from Huacapistana the distance is greater between the lateral plates of the epigynum in posterior view.

Diagnosis. Araneus moretonae differs from *A. acolla* (Fig. 139) and *A. meropes* (Fig. 159) by having rectangular lateral plates of the epigynum almost parallel in position in posterior view (Fig. 143).

Paratypes. PERU *Junín:* Huacapistana, 2500 m, 9♀ (K. Jelski, PAN). *Cusco:* Torontoy Canyon, base of Machupicchu,

2000–2200 m. 19–23 June 1964, ♀ (B. Malkin, AMNH).

Araneus granadensis (Keyserling)
Figures 146–152; Map 3

Epeira granadensis Keyserling, 1864: 86, pl. 4, figs. 7–9, ♀, ♂. Male lectotype, female and two immature paralectotypes, here designated from Santa Fé de Bogotá [Bogotá, Colombia], in BMNH, examined; 1892: 194, pl. 9, fig. 144, ♂, ♀.
Aranea granadensis:—Roewer, 1942: 841.
Neoscona granadensis:—Bonnet, 1958: 3058.

Note. A male lectotype is here designated, as the females are shrivelled and poorly preserved, including the epigynum. The female paralectotypes are undoubtedly the same species. In the vial is also a female *Metepeira*. According to Keyserling's illustration, the female was shrivelled when he illustrated it.

Description. Female from Bogotá. Carapace dark brown with median orange line, sides and eye region orange. Sternum dark brown with median orange streak. Chelicerae mottled; endites dark brown, coxae orange. Legs orange, distal articles ringed dark brown. Dorsum of abdomen dark with indistinct folium, and median anterior light patch (Fig. 149). Venter black and brown with two light bands (Fig. 150). Carapace hairy. Posterior median eyes same diameter as anterior median eyes, lateral eyes 0.8 diameter. Anterior median eyes a little less than 2 diameters apart, a little more than 4 from laterals. Posterior median eyes their diameter apart, a little more than 4 from laterals. Abdomen spherical and hairy (Fig. 149). Total length 10.7 mm. Carapace 4.9 mm long, 4.1 wide. First femur 5.1 mm, patella and tibia 6.6, metatarsus 4.7, tarsus 1.5. Second patella and tibia 5.4 mm, third 3.2, fourth 4.5.

Male from Bogotá. Carapace streaked brown and orange. Labium and endites brown; sternum brown with median yellow streak. Coxae orange; legs orange with darker rings at ends of articles. Dorsum of abdomen whitish with minute, sclerotized, brown spot at base of each of the numerous setae, and small, paired, dusky lines. Venter dark brown enclosing two lighter areas, light on sides. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes a little more than their diameter apart, 1.7 from laterals. Posterior median eyes a little less than their diameter apart, a little less than 3 from laterals. First coxa with hook. Second tibia only slightly thicker than first with short macrosetae. Total length 8.3 mm. Carapace 4.1 mm long, 3.2 wide. First femur 6.2 mm, patella and tibia 7.9, metatarsus 6.3, tarsus 1.8. Second patella and tibia 5.4 mm, third 3.1, fourth 4.5.

Variation. Total length of females 9.7 to 18 mm, of males 8.0 to 8.3.

Diagnosis. Females can be confused with *A. bogotensis* but differ by having the posterior median plate of the epigynum longer than wide (Fig. 147), while that of *A. bogotensis* (Fig. 18) is usually square. Females are further distinguished by the ventral sculpturing, a depression in the lateral plates seen in both ventral (Fig. 146) and posterior view at the ventral end (Fig. 147), and a shorter scape with nearly parallel sides (Fig. 146).

Males differ by having a shorter median apophysis (Fig. 151) and a narrow conductor in the palpus (Fig. 152).

Natural History. The species has been collected on buildings, under eaves, in vegetation, and on a cactus in Bogotá, all at high elevations.

Distribution. Venezuela to Peru (Map 3).

Records. VENEZUELA *Mérida:* La Honda, between Sto. Domingo and Mu-

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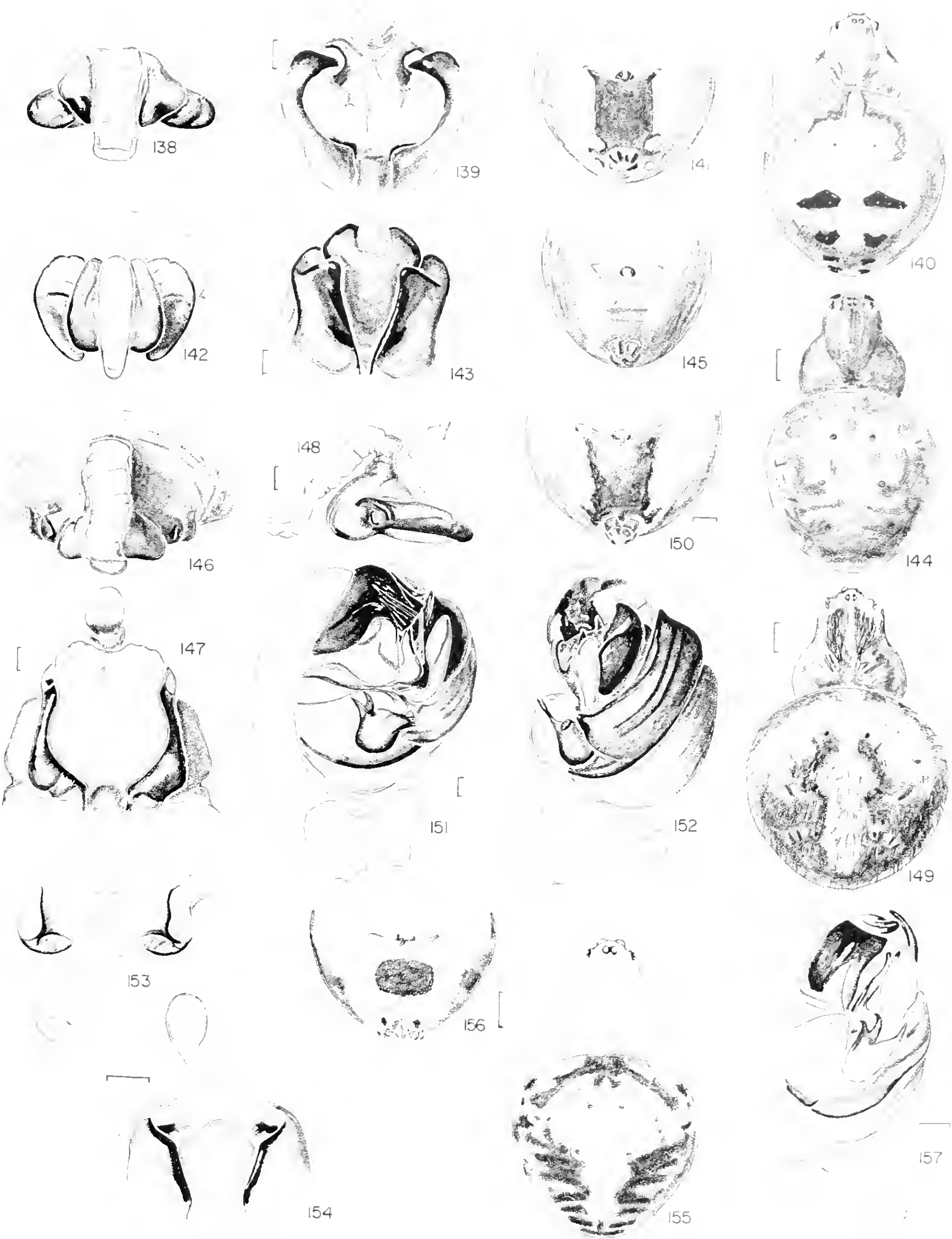
Figures 138–141. *Araneus acolla* n. sp., female. 138. Epigynum, ventral. 139. Epigynum, posterior. 140. Dorsal. 141. Abdomen, ventral.

Figures 142–145. *A. moretonae* n. sp., female. 142. Epigynum, ventral. 143. Epigynum, posterior. 144. Dorsal. 145. Abdomen, ventral.



Figures 146–152. *A. granadensis* (Keyserling). 146–150. Female. 146. Epigynum, ventral. 147. Epigynum, posterior. 148. Epigynum, lateral. 149. Dorsal. 150. Abdomen, ventral. 151, 152. Male, left palpus. 151. Mesal. 152. Ventral.

Figures 153–156. *A. tambopata* n. sp., female. 153. Epigynum, ventral. 154. Epigynum, posterior. 155. Dorsal. 156. Abdomen, ventral.

Figure 157. *A. jamundi* n. sp., male palpus.

Scale lines 1.0 mm, genitalia 0.1 mm.

cubaji, 2600 m, ♀, ♂ (USNM); 11 km SW Sto. Domingo, ♀ (USNM). COLOMBIA *Magdalena:* Cerra Juaneta, Sierra Nevada de Santa Marta, ♀ (JAK); Río Donachui, 3000 m, ♀ (JAK); Río Donachui, 3700 m, ♀ (MCZ); San Sebastian de Rábago, 2000 m, ♀ (AMNH). *Antioquia:* San Pedro, 2000 m, ♀ (MCZ). *Santander:* Río Suárez, 1000 m, ♀ (AMNH); Río Opón, 1000 m, ♀ (AMNH). *Cundinamarca:* Bogotá, ♀, ♂ (MCZ, DU). *Valle:* 21 km W Cali, ♀ (CAS). *Nariño:* La Cruz, 2450 m, ♀ (MCZ). ECUADOR *Pichincha:* Quinche, ♀ (MECN); Puembo, ♀ (MECN); Quito, ♀ (ZMK); 11 km S Cayambe, ♀ (CAS); La Mitad del Mundo, San Antonio de Pichincha, ♀ (MCZ); Cuicocha, Imbabura, 3300 m, ♀ (AMNH); nr. Pomasqui, ♀ (MCZ). *Cotopaxi:* on road from Latacunga to Machai, ♀ (BMNH); Machai to Pedregal, ♀ (BMNH). *Tungurahua:* Ambato, ♂ (CAS). *Chimborazo:* road to Ríobamba, ♀ (BMNH). *El Oro:* Chilla, ♀ (BMNH). PERU *Arequipa:* Atiquipa (Chala), 300 m, ♀ (CAS).

Araneus tambopata new species
Figures 153–156; Map 3

Holotype. Female holotype from Zona Reserva Tambopata, torocha principal: km 3, Madre de Dios, Peru, 21 July 1987 (D. Silva D.), in MHNSM. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, wide black rings around posterior median eyes. Chelicerae, labium, endites, sternum orange. Coxae orange; legs orange with a few scattered black spots; third tarsi and distal half of fourth tibiae and metatarsi black. Dorsum of abdomen black and gray with silver spots (Fig. 155). Venter with a black square, spinnerets orange, anterior ones with a black patch laterally (Fig. 156). Eyes large. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart, 1 from laterals. Posterior median eyes 0.4 their diameter apart, 1.8 from laterals. Abdomen subspherical [damaged] (Fig. 155). Total length 8.8 mm. Carapace 4.0 mm long, 3.1 wide. First femur 4.4 mm, patella and tibia 5.1, metatarsus 3.8, tarsus 1.3. Second patella and tibia 4.5 mm, third 2.7, fourth 4.0.

Note. This species may not belong to the genus *Araneus*. A male is needed for generic placement.

Diagnosis. This species differs from all other Neotropical species by having the scape constricted at the middle, with the distal end wide, and by having a longitudinal groove on each side of the epigynum base (Fig. 153).

Araneus jamundi new species
Figure 157; Map 2

Holotype. Male from Río Jamundí, between Cali and Jamundí, 1000 m, Valle, Colombia, 1973 (W. Eberhard), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace orange with dusky patch covering eyes and coming to a point in thoracic depression. Chelicerae, labium, endites, sternum, coxae, and legs light orange. Abdomen white; venter with row of white pigment spots behind genital groove, and another in front of spinnerets. Thoracic depression a cross with lateral branches pointing posteriorly. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes slightly more than their diameter apart, the same from laterals. Posterior median eyes 0.4 their diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first. Abdomen oval, pointed behind. Total length 5.2 mm. Carapace 2.7 mm long, 2.1 wide. First femur 4.2 mm, patella and tibia 5.0, metatarsus 3.9, tarsus 1.1. Second patella and tibia 3.8 mm; third 1.9, fourth 2.7.

Diagnosis. The male of this species is distinguished from other known males by the thin elongate embolus and the pointed lateral end of the median apophysis (Fig. 157).

Araneus meropes (Keyserling)
Figures 158–167; Map 3

Epeira meropes Keyserling, 1865: 825, pl. 19, figs 6, 7, ♂. Male holotype from New Granada [Spanish

colony of Colombia and Panama], in BMNH, examined; 1892: 139, pl. 7, fig. 102, ♂.

?*Epeira lechugalensis* Keyserling, 1883, 195, pl. 15, fig. 1, ♀. Female holotype from Lechugal [Puestó Lechugal, Tumbes, 03°37'S, 80°12'W], Peru, in PAN, lost; 1892: 191, pl. 9, fig. 142, ♀. DOUBTFUL NEW SYNONYMY.

Araneus bourgeoisi Berland, 1913: 93, pl. 9, figs. 44, 45, ♀. Female holotype from Pinllar [Cerro Pinllar], Ecuador, lost (not in MNHN). Bonnet, 1955: 448. NEW SYNONYMY.

Aranea plesia Chamberlin, 1916: 253, pl. 19, fig. 5, ♀. Female holotype from Sorontoy, 2300 m [Torontoy, Dpto. Cusco, 13°10'S,72°30'W], Peru, in MCZ, examined. Roewer, 1942: 850. NEW SYNONYMY.

Aranea bourgeoisi:—Roewer, 1942: 838.

Aranea lechugalensis:—Roewer, 1942: 846.

Aranea meropes:—Roewer, 1942: 846.

Araneus lechugalensis:—Bonnet, 1955: 528.

Araneus meropes:—Bonnet, 1955: 543.

Araneus plesius:—Bonnet, 1955: 567.

Note. I previously (Levi, 1973) synonymized the name *meropes* with *thaddeus*; this was an error. Keyserling's illustration of *Epeira lechugalensis* may be this species; perhaps the scape was torn off in his specimen. The proportions of the epigynum illustrated by Berland makes it possible to identify *Araneus bourgeoisi.*

Description. Female from Sierra Nevada de Santa Marta, Colombia. Carapace brownish orange, sides of head and thorax brown. Chelicerae brownish orange. Labium, endites brown. Sternum dark brown. Coxae orange; legs dark brown, except proximal parts of third and fourth femora orange. Dorsum of abdomen with light folium marks on dark brown (Fig. 164); venter with a median dark band, a light brown band on each side, and sides dark (Fig. 165). Posterior median eyes same diameter as anterior medians, laterals 0.9 diameter. Anterior median eyes 1 diameter apart, 1.7 from laterals. Posterior median eyes slightly less than their diameter apart, 2.2 from laterals. Abdomen subspherical (Fig. 164). Total length 8.7 mm. Carapace 3.2 mm long, 2.7 wide. First femur 3.4 mm, patella and tibia 4.1, metatarsus 2.9, tarsus 1.0; Second patella and tibia 3.2 mm, third 1.9, fourth 2.9.

Male from Sierra Nevada de Santa Marta, Colombia. Color lighter than in female, legs ringed, and abdominal light markings dark and indistinct. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 1.2 diameters apart, 1.3 from laterals. Posterior median eyes 1 diameter apart, 3 from laterals. Endite with blunt tooth. First coxa with hook. Second tibia slightly thicker than first. Abdomen oval. Total length 5.5 mm. Carapace 2.8 mm long, 2.3 wide. First femur 4.9 mm, patella and tibia 5.7, metatarsus 4.6, tarsus 1.1. Second patella and tibia 3.8 mm, third 2.1, fourth 2.3.

Variation. The measurements above are of specimens from northern Colombia. The measurements of the male type of *Epeira meropes* are total length 4.3 mm; carapace 2.1 mm long, 1.7 wide; first femur 3.4 mm, patella and tibia 4.1, metatarsus 2.9, tarsus 0.9; second patella and tibia 2.8 mm, third 1.4, fourth 2.2. A male from Peru measured total length 5.4 mm; carapace 2.5 mm long, 1.9 wide; first femur 2.4 mm, patella and tibia 3.1, metatarsus 2.1, tarsus 0.8; second patella and tibia 2.5 mm, third 1.4, fourth 2.1. A male from Antioquia, Colombia, measured total length 3.8 mm; carapace 2.1 mm long, 1.6 wide; first femur 2.9 mm, patella and tibia 3.2, metatarsus 2.3, tarsus 0.8; second patella and tibia 2.0 mm, third 1.3, fourth 1.9.

The eye ratios of three males (the holotype of *meropes*; specimen from Antioquia Dept., Colombia; specimen from Magdalena Dept., Colombia) were as follows: posterior medians, 1, 0.8, 0.8 diameter of anterior medians, laterals 1, 0.6, 0.5 diameter. The anterior medians are 1.5, 1, 1.2 diameters apart; 1.5, 1+, 1.3 diameters from laterals. The posterior median eyes are 1, −1, 1 diameter apart; 3, 2, 3 diameters from laterals.

Total length of females 5.7 to 9.5 mm, of males 3.8 to 5.5 mm. The smallest female came from Peru, the largest from Argentina, but differences in size are individual, not regional.

There is considerable variation among specimens and they were first thought to belong to several species. In females there is variation in dorsal-abdominal and car-

apace pattern, in size and relative leg length, and in the shape of the posterior median plate of the epigynum. Males differ in relative size of the palpal tibia (small in central specimens, large in southern ones), and the median apophysis of the palpus differs in length and in the shape of its distal tip.

Diagnosis. Females can be separated from *A. koepckeorum* (Fig. 168) by the smaller lateral lobes in ventral view of the epigynum, containing smaller depressions (Figs. 158, 160, 162).

The male can be separated from others by the relatively short lateral tail of the median apophysis (Fig. 166), the stalked bent conductor (Fig. 167), and the laterally curved embolus, which has a soft area toward the median (Fig. 166). The males have shorter legs than the males of the similar *A. koepckeorum*.

Natural History. Some specimens in collections came from wasp nests. Others came from spiny clump-forming bromeliads in northern Colombia, all ages side by side. One spider was found in a bromeliad, in the growing tip in small leaves. Several leaves are bound together with strong silk. The web of a large female is above the retreat and connected to surrounding vegetation with a line down to the bromeliad, where the spider often retreats deep inside. Adults are drab, but juveniles exhibit a variety of colors (J. Kochalka, personal communication). Still other specimens came from a bamboo cloud forest, ruins at Machupicchu, and a forest in Argentina; all came from high elevations.

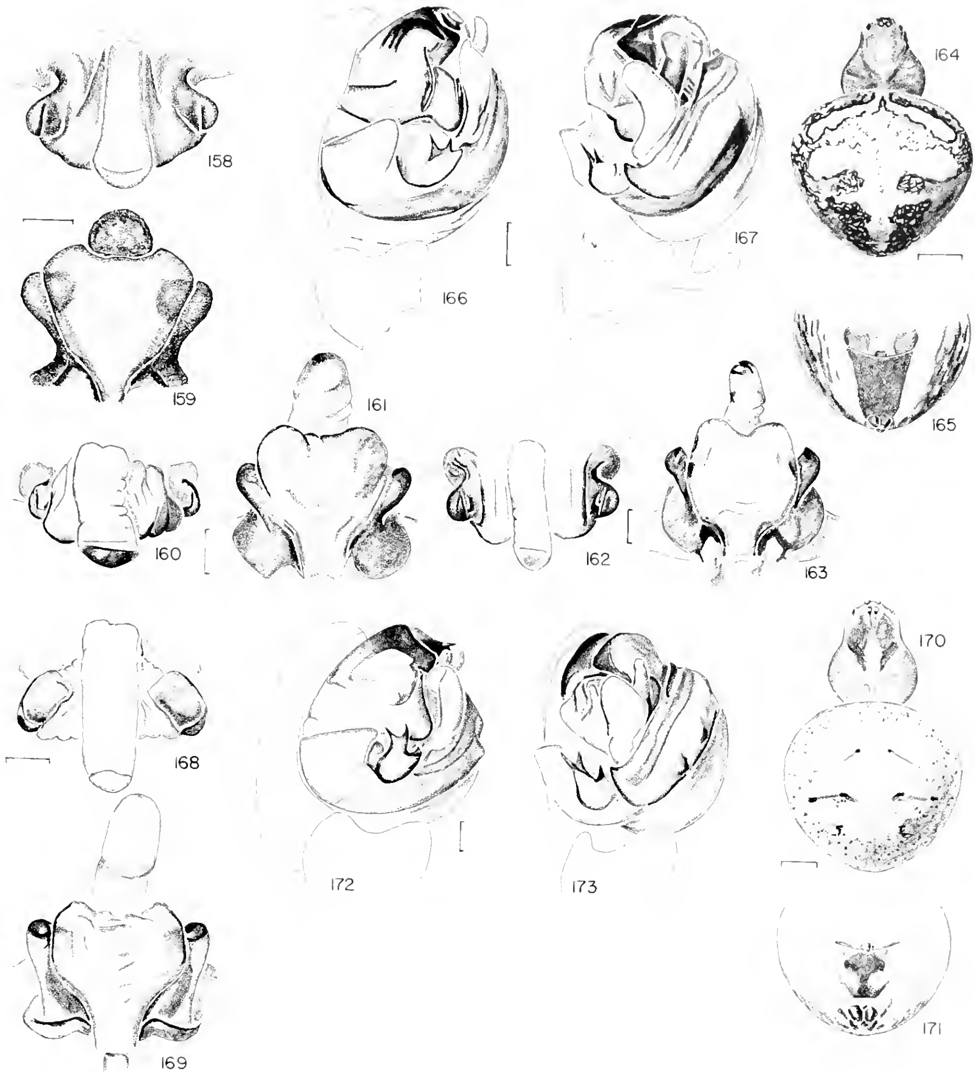
Distribution. Northern Colombia to northern Argentina (Map 3).

Records. COLOMBIA *Magdalena:* Sierra Nevada de Santa Marta: East Cerro Kennedy, 2240 m, ♀, ♂ (MCZ); Cerro Las Palomitas, 2500 m, ♀ (JAK); Casa Antonio, Loma Cebollita, 2700 m, ♀, ♂ (USNM, AMNH, MCZ); Mt. San Lorenzo, Santa Marta, 2250 m, ♀ (MCZ). *Antioquia:* Medellín Valley, 1700–1900 m, ♀, ♂ (MCZ); Peñol, 2100 m, ♀, ♂ (MCZ); Giraldo, 2100 m, ♀ (MCZ); Santa Rosa de Osos, ♀ (MNHMC). *Santander:* Río Suárez, 800–1000 m, ♀ (AMNH). *Valle:* 10 km W Cali, ♀ (MCZ); above Fidelia, 2000 m, ♀ (MCZ). *Nariño:* La Cruz (CV). *Putumayo:* Sibundoy, 2200 m, ♀ (MCZ). *Caquetá:* Río Orteguaza, ♂ (AMNH). ECUADOR *Pichincha:* Tumbaco, ♀ (MECN); nr. Pomasquí, ♀, ♂ (MCZ). *Morona-Santiago:* Sucúa, 1000 m, ♀ (MCZ). *Azuay:* S Cuenca, 2500–2800 m, ♂ (MCZ); Cuenca, ♀, ♂ (MECN); Cuenca, ♀ (MCZ, CAS); 30 km NE Cuenca, ♀ (CAS). PERU *Piura:* Huara, 3000 m, ♀ (CAS); *Cajamarca:* Llama, 2200 m, ♀ (CAS); Montana de Nancho, 2400 m, ♀ (PAN). *Lima:* Río Rímac at Matucana, 2400 m, ♀ (CAS); Matucana, ♀ (CU); Canta, 2800 m, ♀ (CAS). *Junín:* vicinity of Viena, 2600 m, ♂ (BMNH); Pumamarca, ♀ (PAN); Amable María, ♀ (PAN). *Cusco:* Urubamba, 2800 m, ♀, ♂ (MCZ); Machupicchu, 2400 m, ♀ (MCZ, AMNH). *Puno:* Limbani, Carabaya, 2900 m, ♀, ♂ (BMNH); Angualani, nr. Limbani, ♀ (BMNH). ARGENTINA *Salta:* Rd. 33 from Chicoana to Cachi, ca. 12 km W El Caril, 18 Mar. 1988, 3♀ (F. Coyle, R. Bennett, P. A. Goloboff, MCZ).

Araneus koepckeorum new species
Figures 168–173; Map 3

Holotype. Female from Miraflores, Lima, Peru, 6 Feb. 1965, in house and garden (H. Levi), in MCZ. This species is named after H. W. and M. Koepcke, former hosts of the Humboldt house in Miraflores and proponents of Peruvian biological studies.

Description. Female. Carapace orange, sides of head brown, sides of thorax dark orange. Chelicerae dark orange. Labium, endites brown with lighter margin. Sternum dark brown with a median, light, longitudinal band enclosing some white pigment. Coxae light orange. Legs light orange with narrow brown rings. Dorsum of abdomen light brown, with black dots and paired dark transverse lines (Fig. 170). Venter light, with a black band between epigynum and spinnerets enclosing pairs of light patches (Fig. 171); spinnerets dark brown. Posterior median eyes same diameter as anterior medians, anterior lat-



Figures 158–167. *Araneus meropes* (Keyserling). 158–165. Female. 158, 160, 162. Epigynum, ventral. 159, 161, 163. Epigynum, posterior. 158, 159 (Torontoy, Dpto. Cusco, Peru). 160, 161 (Dpto. Magdalena, Colombia). 162, 163 (Machupicchu, Cusco, Peru). 164. Dorsal. 165. Abdomen, ventral. 166, 167. Male, left palpus. 166. Mesal. 167. Ventral.

Figures 168–173. *A. koepckeorum* n. sp. 168–171. Female. 168. Epigynum, ventral. 169. Epigynum, posterior. 170. Dorsal. 171. Abdomen, ventral. 172. Male palpus, mesal. 173. Ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.

erals 0.7 diameter, posterior laterals 0.8. Anterior median eyes 1.2 diameters apart, 2 from laterals. Posterior median eyes their diameter apart, slightly more than 3 from laterals. Abdomen subspherical, widest anteriorly (Fig. 170). Total length 7.5 mm. Carapace 3.2 mm long, 2.6 wide. First femur 4.2 mm, patella and tibia 4.7, meta-

tarsus 3.4, tarsus 1.2. Second patella and tibia 3.7 mm, third 2.1, fourth 3.3.

Male. Coloration as in female. Chelicerae distally swollen. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.2 diameters apart, 1.6 from laterals. Posterior median eyes their diameter apart, almost 3 from laterals. Endite with tooth. Coxal hook forming a blunt spine. Femoral groove very small. Second tibia thinner than first, not modified. Abdomen oval, widest anteriorly. Total length 5.4 mm. Carapace 2.7 mm long, 2.3 wide. First femur 5.3 mm, patella and tibia 6.1, metatarsus 5.2, tarsus 1.4. Second patella and tibia 4.3 mm, third 2.2, fourth 3.4.

Variation. Total length of females 4.7 to 8.4 mm, of males 4.7 to 5.5.

Diagnosis. The female can be distinguished from that of *A. meropes* (Figs. 158, 159) by the larger lateral lobes in ventral view of the epigynum (Fig. 168). The male palpus is similar to that of *A. meropes* (Figs. 166, 167), but the shape of the conductor is more rounded (Figs. 172, 173). The legs of the male are much longer than those of *A. meropes*: in *A. koepckeorum* males, the length of the first femur is equal to the total length of the spider and the first patella and tibia are 2.2 times the length of the carapace, while in *A. meropes* the length of the first femur is 1.3 times that of the carapace, and the first patella and tibia are 1.5 times the length of the carapace.

Natural History. The species has been collected from a garden and from a cotton field near Lima.

Distribution. Mostly from lower elevations, Peru (Map 3).

Paratypes. PERU *Cajamarca:* Montaña di Nancho, 2400 m, ♀ (K. Jelski, J. Sztolcman, PAN). *Lima:* Canta, 6 Apr. 1985, ♂ (V. Pacheco, MHNSM); Lima, 9♀ (K. Jelski, J. Sztolcman, PAN); Quebrada Verde, Nov. 1948, 8♀, ♂ (W. Weyrauch, CAS); Canta, Río Chillón, 2800 m, 12 May 1951, 5♀ (W. Weyrauch, CAS). *Cusco:* Urubamba, Nov. 1986, ♀ (E. Yabar, MHNSM). *Arequipa:* Mollendo, Loma Zone, 19 Nov. 1950, 4♀, ♂ (E. S. Ross, A. E. Michelbacher, CAS); Atiquipa (Chala) 500 m, 11 Dec. 1951, ♀ (W. Weyrauch, AMNH); Arequipa, 4 Apr. 1953, 2♀ (I. Brownlee, CAS); Capac (Chala), 200 m, 9 Dec. 1951, ♀ (W. Weyrauch, AMNH); Atiquipa (Chala) 200 m, 11 Dec. 1951, ♀, 2♂ (W. Weyrauch, CAS, MCZ).

Araneus stabilis (Keyserling)
Figures 174–178; Map 3

Epeira stabilis Keyserling, 1892: 213, pl. 10, fig. 158, ♀, ♂. One female lectotype, one male paralectotype here designated from Rio Minas, Est. Espírito Santo, Brazil, in BMNH, examined.
Aranea stabilis:—Roewer, 1942: 853.
Araneus stabilis:—Bonnet, 1955: 603.

Figures 174–178. *Araneus stabilis* (Keyserling). 174–176. Female. 174. Epigynum, ventral. 175. Epigynum, posterior. 176. Dorsal. 177. Abdomen, ventral. 178. Male, left palpus.

Figures 179–183. *A. fronki* n. sp. 179–182. Female. 179. Epigynum, ventral. 180. Epigynum, posterior. 181. Dorsal. 182. Abdomen, ventral. 183. Male palpus.

Figures 184–187. *A. beebei* n. sp., female. 184. Epigynum, ventral. 185. Epigynum, posterior. 186. Dorsal. 187. Abdomen, ventral.

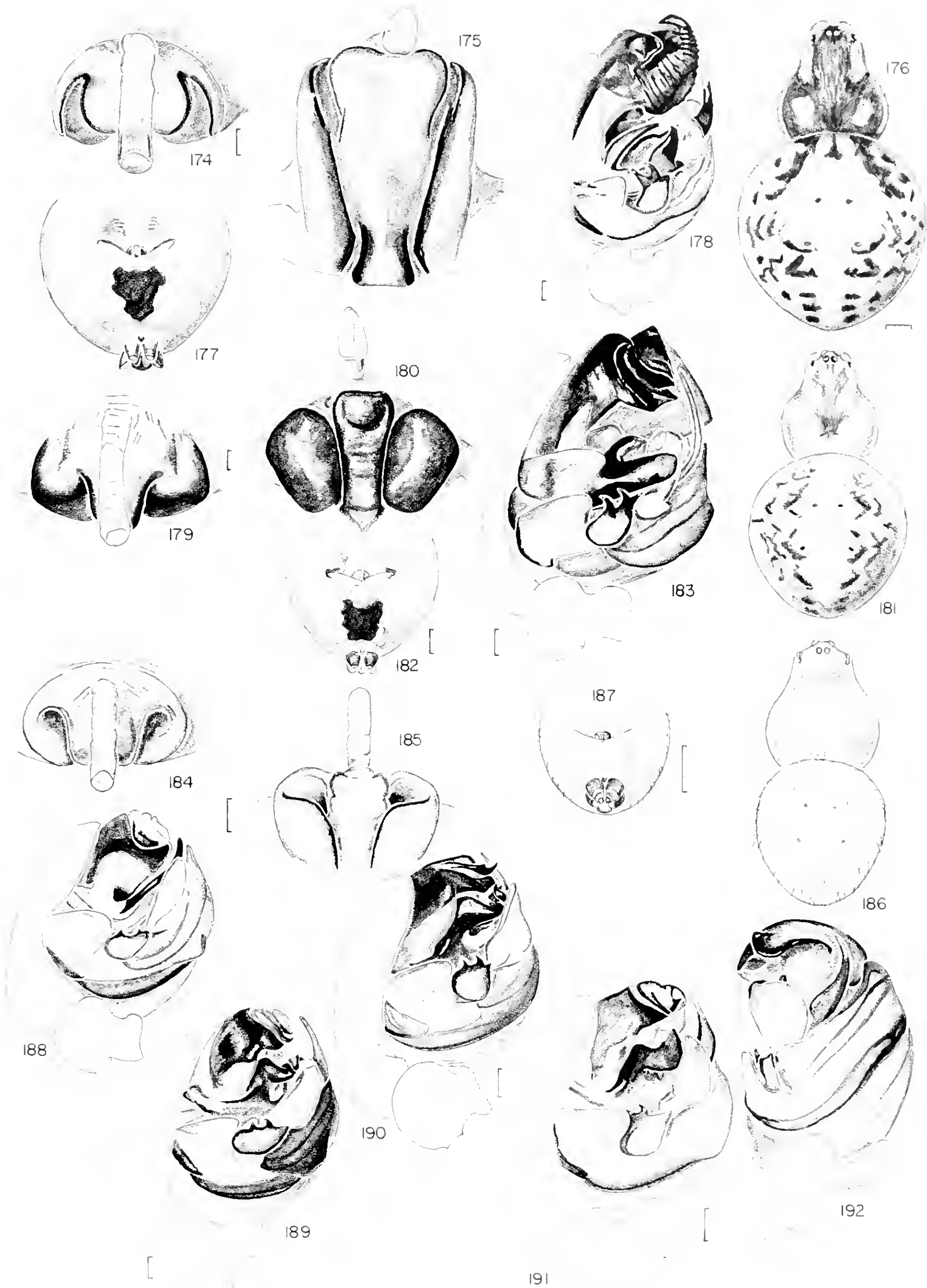
Figure 188. *A. cohnae* n. sp., male palpus.

Figure 189. *A. matogrosso* n. sp., male palpus.

Figure 190. *A. carimagua* n. sp., male palpus.

Figures 191, 192. *A. gerais* n. sp., male palpus. 191. Mesal. 192. Ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.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Description. Female from Rio de Janeiro. Carapace dark brown, with two pairs of light patches and white setae, rim of thorax light. Labium brown, sternum orange with dark patch on each side. Coxae light orange; legs orange with dark brown rings and patches. Dorsum of abdomen with three dark anterior marks and paired posterior marks (Fig. 176); venter with a triangular black patch (Fig. 177). Posterior median and lateral eyes 0.8 diameter of anterior median eyes. Anterior median eyes their diameter apart, 1.2 from laterals. Posterior median eyes 0.5 diameter apart, 2 from laterals. Abdomen spherical (Fig. 176). Total length 12.5 mm. Carapace 5.3 mm long, 4.6 wide. First femur 6.2 mm, patella and tibia 7.2, metatarsus 5.7, tarsus 1.8. Second patella and tibia 6.6 mm, third 4.0, fourth 5.9.

Male from Curitiba. Lighter than female. Carapace dark orange with symmetrical dusky marks. Chelicerae, labium, endites dark orange. Sternum, orange. Coxae orange; legs orange with dark rings. Dorsum of abdomen with three black marks on anterior margin, a black outline of folium posteriorly. Posterior median and anterior lateral eyes 0.7 diameter of anterior median eyes, posterior laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart, 0.7 from laterals. Posterior medians 0.5 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first. Abdomen oval. Total length 5.8 mm. Carapace 3.2 mm long, 2.7 wide. First femur 4.8 mm, patella and tibia 5.9, metatarsus 5.0, tarsus 1.5. Second patella and tibia 4.6 mm, third 2.6, fourth 3.6.

The photograph of a female shows the carapace to be black with white setae and the abdomen with median reddish folium, white patches between it and the black marks, and the abdomen sides to be white and black.

Note. Males and females were matched by Keyserling. Females of one collection were collected with males of *A. workmani*; no other females have been collected with males.

Variation. Total length of females 7.5 to 12.5 mm, of males 4.8 to 7.7. Most females have the carapace dark with paired light patches, the abdomen relatively light.

Diagnosis. The female is easily separated from those of similar species by the epigynum, which has a pointed slit on each side in ventral view (Fig. 174) and a median plate (in posterior view), which is about twice as long as wide (Fig. 175). No other species has the median plate so long.

The male differs from that of *A. fronki* (Fig. 183) by having the spines of the median apophysis different in shape, a differently shaped embolus, and a bulging, striated terminal apophysis (Fig. 178).

Natural History. Specimens have been collected from a forest edge in the Rio de Janeiro Botanical Garden.

Distribution. From southern Bahia State, Brazil, to Buenos Aires Province, Argentina (Map 3).

Records. BRAZIL *Bahia:* Fazenda Matia, Camacan [?], ♀ (MCN). *Espírito Santo:* Espírito Santo, ♂ (BMNH). *Rio de Janeiro:* Rio de Janeiro, Jardim Botânico, 3♀ (MCZ, MNRJ); Parque Nacion. Tijuca, ♀ (MCZ). *São Paulo:* Monte Alegre, Amparo, 8 imm., 2♂ (MZSP); Ilha da São Sebastião, ♀ (MZSP); São Paulo, ♀, ♂ (AMNH, MZSP); Barueri, ♀ (MZSP); Cocaia, Santo Amaro, 2♀ (MZSP); Mauá, 4♀ (MZSP). *Paraná:* Curitiba, ♀ (MNRJ); Iguatemi, ♂ (MCN); Vila Velha, 2♀ (MZSP). *Santa Catarina:* Pinhal, 4♀ (AMNH). *Rio Grande do Sul:* Cazuza Ferreira, ♀ (MCN); Morro do Itacolomi Gravataí, ♂ (MCN); Porto Alegre, ♂ (MCN); Triunfo, ♂ (MCN). ARGENTINA *Misiones:* Gral. M. Belgrano, ♂ (MEG).

Araneus fronki new species
Figures 179–183; Map 3

Holotype. Male holotypes from Lavras, Est. Minas Gerais, Brazil, 29 Mar. 1979 (W. D. Fronk), MZSP, ex MCZ. The species is named after the collector.

Description. Female from Ouro Prêto. Carapace orange with darker branching patch and dark patches on sides of thorax. Chelicerae orange. Labium, endites brown. Sternum with orange longitudinal band,

sides brown. Coxae orange; legs orange with brown patches. Dorsum of abdomen light with dusky marks outlining a folium (Fig. 181); venter with black square and white pigment spots between square and epigynum (Fig. 182). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 0.6 diameter apart, 1.1 from laterals. Posterior median eyes 0.7 diameter apart, 2.3 from laterals. Abdomen subspherical (Fig. 181). Total length 10.5 mm. Carapace 4.5 mm long, 3.6 wide. First femur 5.2 mm, patella and tibia 6.3, metatarsus 5.1, tarsus 1.7. Second patella and tibia 5.8 mm, third 3.5, fourth 5.0.

Male from Diamantina. Coloration as in female, but legs ringed. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5. Anterior median eyes 0.6 diameter apart, 0.6 from laterals. Posterior median eyes 0.5 diameter apart, 1.5 from laterals. Endite without tooth. First coxa with hook. Second tibia only slightly thicker than first with some macrosetae on mesal side. Abdomen oval, pointed behind. Total length 5.5 mm. Carapace 2.7 mm long, 2.3 wide. First femur 4.9 mm, patella and tibia 5.8, metatarsus 5.6, tarsus 1.3. Second patella and tibia 4.2 mm, third 2.4, fourth 3.4.

Variation. The epigynum may have the median plate heavily sclerotized and black (Fig. 180) or lightly sclerotized and light in color. Total length of females 7.3 to 10.5 mm, of males 5.5 to 5.6. The three spines of the median apophysis vary slightly in their distance from each other and in the sizes of the notches between them.

Diagnosis. Females are distinguished from other species by the narrow posterior median plate (Fig. 180), which bulges posteriorly under the scape (Fig. 179). Males are distinguished from others by the nearly circular median apophysis with three spines and the embolus, which surrounds the conductor (Fig. 183).

Distribution. Minas Gerais, Brazil (Map 3).

Paratypes. BRAZIL *Minas Gerais:* Ouro Prêto, Apr. 1954, 2♀ (N. L. H. Kraus, AMNH); Minha Serinha, Diamantina, Dec. 1944, 6♀, ♂; Jan.–Mar. 1945, ♀; 1945, 3♂, imm. (E. Cohn, AMNH).

Araneus beebei new species
Figures 184–187; Map 3

Holotype. Female holotype from Rancho Grande near Maracay, Aragua, Venezuela, 24 Aug. 1946 (W. Beebe), in AMNH. The species is named after the collector and explorer William Beebe.

Description. Female. Carapace orange with some darker orange marks, no black pigment around eyes. Chelicerae, labium, endites, sternum, coxae and legs orange. Dorsum of abdomen white (Fig. 186); venter with square white patch, spinnerets brown (Fig. 187). Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1 diameter apart, 1.6 from laterals. Posterior median eyes 0.5 their diameter apart, 2.7 from laterals. Abdomen oval with long hair (Fig. 186). Total length 5.4 mm. Carapace 2.9 mm long, 2.4 wide. First femur 3.6 mm, patella and tibia 4.1, metatarsus 3.1, tarsus 1.1. Second patella and tibia 3.5 mm, third 2.0, fourth 3.0.

Diagnosis. This species is distinguished from the Brazilian *A. fronki* by a different curvature of the median edge of the lateral plates of the epigynum in posterior view (Fig. 185), and a median plate wider than the laterals in ventral view (Fig. 184).

Araneus cohnae new species
Figure 188; Map 3

Holotype. Male holotype from Minha Serinha, Diamantina, Minas Gerais, Brazil, Jan.–Mar. 1945 (E. Cohn), in AMNH. The species is named after the collector.

Description. Male. Carapace glabrous orange-brown. Chelicerae, labium, endites, sternum, and coxae orange. Legs orange-brown, faintly ringed on venter. Dorsum of abdomen with a white patch which narrows posteriorly; sides gray posteriorly with indistinct dark transverse bars on each side of white patch; venter gray with white

spot on each side. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes slightly more than 1 diameter apart, 1 from laterals. Posterior median eyes 0.6 diameter apart, 2 from laterals. Endite with blunt tooth. Palpal patella with one macroseta. First coxa without hook. Second tibia thicker than first. Abdomen oval. Total length 3.4 mm. Carapace 1.9 mm long, 1.5 wide. First femur 2.3 mm, patella and tibia 2.5, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.1 mm, third 1.1, fourth 1.6.

Note. This might be the male of *A. bandelieri.*

Diagnosis. This male is distinguished from males of *A. carimagua, A. matogrosso,* and *A. gerais,* which also lack a coxal hook, by the straight rod-like embolus (Fig. 188). *Araneus cohnae* differs from males of all other Neotropical *Araneus* species in having only one macroseta on the palpal patella.

Araneus matogrosso new species
Figure 189; Map 3

Holotype. Male holotype from 260 km N of Xavantina, Est. Mato Grosso [12°49'S, 51°46'W], 400 m el., Brazil, in gallery forest, Feb.–Apr. 1969 (Xavantina–Cachimbo Exped.), in MZSP, ex MCZ. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace dark orange with a dark brown median streak from eye region to cross-shaped thoracic mark, posterior median eyes on a transverse, oval black mark. Chelicerae, labium, endites orange. Sternum orange. Coxae orange; legs dark orange with indistinct brown rings. Dorsum of abdomen with anterior dark mark on each side and posterior indistinct black folium on gray; venter with transverse black mark, on each side of which is a white spot. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.4 diameter, posterior laterals 0.5. Anterior median eyes 1 diameter apart, 1 from laterals. Posterior median eyes 0.6 diameter apart, 2.7 from laterals. Endite without tooth. First coxa without hook. Second tibia very slightly thicker than first with short macrosetae. Abdomen oval, pointed behind. Total length 7.7 mm. Carapace 3.9 mm long, 3.2 wide. First femur 5.2 mm, patella and tibia 6.5, metatarsus 5.2, tarsus 1.6. Second patella and tibia 5.2 mm, third 2.7, fourth 4.2.

Diagnosis. This male is close to those of the Colombian species *A. carimagua* and *A. gerais* and, as these two, has a bulky twisted embolus and a median apophysis with two teeth and one blunt lateral tooth. It differs from both by having a longer median apophysis and a differently shaped terminal apophysis (Fig. 189). The embolus of *A. gerais* is wider than that of *A. matogrosso.*

Araneus carimagua new species
Figure 190; Map 3

Holotype. Male from Carimagua [04°35'N, 71°20'W] 100 m, Meta, Colombia, Oct. 1973 (W. Eberhard), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace orange with median black patch; thoracic depression a cross. Chelicerae, labium, endites, sternum, coxae orange. Legs orange with black ring on distal end of tibiae. Dorsum of abdomen white with a black patch anterior on each side and a black outline of folium posteriorly; venter light without pigment except for dusky transverse mark through middle. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.7 diameter apart, 0.6 from laterals. Posterior median eyes 0.6 their diameter apart, slightly more than 2 from laterals. Endite with indistinct, flat tooth. First coxa without hook. Second tibia thinner than first. Abdomen oval, pointed behind. Total length 5.1 mm. Carapace 2.9 mm long, 2.1 wide. First femur 3.5 mm, patella and tibia 4.1, metatarsus 3.3, tarsus 1.1. Second patella and tibia 3.4 mm, third 1.7, fourth 2.5.

Diagnosis. The male differs from that of *A. matogrosso* (Fig. 189) by having the

median apophysis round (Fig. 190) rather than longer than wide.

Araneus gerais new species
Figures 191, 192; Map 3

Holotype. Male holotype from Monte Santo, Est. Minas Gerais, Brazil, 1–5 Apr. 1942 (S. S. Pereira), in MZSP no. 9602. The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange with a narrow, median, longitudinal dark streak. Chelicerae, endites, labium, and sternum light orange. Legs yellowish-white. Dorsum of abdomen with a median white pigment band and two anterior black marks on margin, sides and venter whitish. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes slightly less than their diameter apart, 0.6 from laterals. Posterior median eyes 0.4 diameter apart, 1.3 from laterals. Endite without tooth; no tooth on palpal femur. First coxa without hook. Second tibia as thick as first. Abdomen oval, pointed behind. Total length 4.8 mm. Carapace 2.4 mm long, 2.0 wide. First femur 3.5 mm, patella and tibia 4.1, metatarsus 3.4, tarsus 1.1. Second patella and tibia 3.4 mm, third 1.7, fourth 2.5.

Diagnosis. This species is distinguished from *A. matogrosso* (Fig. 189) by having the median apophysis as long as wide (Fig. 191), from *A. carimagua* and *A. matogrosso* by the distally wider embolus (Fig. 191).

Araneus expletus (O. P.-Cambridge)
Figures 193–210; Map 3

Epeira expleta O. P.-Cambridge, 1889: 25, pl. 6, fig. 11, ♀. Female holotype from Senahú, Vera Paz [Verapaz], Guatemala, in BMNH, examined.

Epeira smithi O. P.-Cambridge, 1898: 280, pl. 37, fig. 4, ♀. Female holotype from Orizaba, Veracruz, Mexico, in BMNH, examined. NEW SYNONYMY.

Neosconella styligera F. P.-Cambridge, 1904: 475, pl. 45, fig. 1, ♂. Male holotype from Guatemala in BMNH, examined (not female paratype). NEW SYNONYMY.

Neosconella expleta:—F. P.-Cambridge, 1904: 476, pl. 45, fig. 7, ♀. Bonnet, 1958: 3061.

Neosconella guttata F. P.-Cambridge, 1904: 477, pl. 45, fig. 9, ♀. Female holotype, juvenile paratype from Omilteme [Omiltemi, Guerrero, 16 km WSW Chilpancingo], Mexico, in BMNH, examined. Bonnet, 1958: 3061. NEW SYNONYMY.

Aranea smithi:—F. P.-Cambridge, 1904: 511, pl. 49, fig. 1, ♀. Roewer, 1942: 853.

Araneus gratuitus Petrunkevitch, 1911: 294. New name for *Neosconella guttata* in combination with *Araneus*, thought to be preoccupied by *Epeira guttata* Keyserling. Kraus, 1955: 22, figs. 59, 61, ♀. NEW SYNONYMY.

Aranea explecta [*sic*]:—Roewer, 1942: 842.

Aranea gratuita:—Roewer, 1942: 843.

Araneus smithi:—Bonnet, 1955: 601.

Note. The type specimen of *expleta* (Figs. 193, 194, 201) was on a pin in alcohol; the pin was carefully removed. The holotype of *E. smithi* is relatively large and dark colored (Figs. 195, 196, 202, 205). Figures 208 and 210 were made from the holotype of *N. styligera*.

Description. Female holotype of *expleta*. Carapace dark brown. Chelicerae, labium, endites brown. Sternum dark brown. Coxae dusky yellow; legs dusky yellow to orange with indistinct darker rings. Dorsum of abdomen with anterior orange area surrounded by black, posterior black with paired light patches (Fig. 201). Venter dark gray with a light band on each side; light bands continue anteriorly around pedicel and curve toward each other but do not meet. Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.6. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.3 diameter apart, slightly more than 2 from laterals. Abdomen subspherical (Fig. 201). Total length 7 mm. Carapace 3.1 mm long, 2.4 wide. First femur 3.5 mm, patella and tibia 4.1, metatarsus 2.9, tarsus 1.1. Second patella and tibia 3.4 mm, third 2.0, fourth 3.0.

Male holotype of *styligera*. Carapace dark, dusky brown. Sternum dark with median yellow streak that is wide in front, narrow behind. Legs ringed. Dorsum of abdomen with four white anterior patches, paired dark posterior marks. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes a little more than their diameter

apart, the same from laterals. Posterior median eyes 0.4 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia with short macrosetae. Total length 6.5 mm. Carapace 3.6 mm long, 2.9 wide. First femur 5.7 mm, patella and tibia 6.4, metatarsus 4.6, tarsus 1.4. Second patella and tibia 5.0 mm, third 2.6, fourth 3.9.

Variation. This species is unusually variable, less in coloration than in size and shape of the lateral plates of the epigynum in ventral view (Figs. 193, 195, 197, 199) and the shape of the median apophysis of the male palpus (Figs. 208, 209). It was first thought that there were five or six species, but as specimens accumulated, their separation became increasingly difficult. Total length of females 5.8 to 12 mm, of males 4.5 to 7.7.

Diagnosis. Females differ from *A. guatemus* (Fig. 211) and *A. pegnia* (Fig. 228) by the shape and length of the scape (Figs. 193, 195, 197, 199), from *A. pegnia* by the shape of the lateral plates in ventral view (Figs. 193, 195, 197, 199).

Males of *A. expletus* have a fish-tailed median apophysis (Figs. 208, 210), while *A. pegnia* males (Fig. 234) lack the fish-tail. The embolus has a distal median notch and a rod-shaped lamella (Figs. 208, 209).

Natural History. Females have been collected along roadsides and forest edges, and in a tropical rain forest in Chiapas. Eberhard (in letter) reports that the silk of the orb is yellow.

Distribution. Tamaulipas, Mexico, to western Panama at intermediate elevations (Map 3).

Records. MEXICO *Tamaulipas:* Santa Gracia [?] (MCZ). *Distríto Federal:* W Río Frío, 2900 m, ♀ (AMNH). *Morelos:* Cuernavaca ♀, 2♂ (AMNH). *Puebla:* Huauchinango, ♀, ♂ (AMNH). *Veracruz:* Estac. de Biología Tropical, nr. La Palma, ♀, 2♂ (MCZ) *Oaxaca:* Juquila, ♀ (AMNH). *Tabasco:* Teapa, 2♀ (BMNH). *Chiapas:* Oaxaca border 21 km W Rizo de Oro, ridge SE Cerro Baúl, 1615 m, ♀, ♂ (CAS); 76 km S Palenque on rd. to Ococingo, 700 m, ♀ (MCZ); Selva de Ocote, 32 km NW Ocozocoautla, 762 m, ♀ (CAS). GUATEMALA *Quiché:* 5 km N Chichicastenango, ♀ (AMNH). HONDURAS *Atlantida:* Lancetilla, mountain trail, 400 m, ♀ (MCZ). EL SALVADOR *Libertad:* Volcán de San Salvador, 2♀ (SMF). COSTA RICA *San José:* San José zoological park, 2♀ (AMNH, USNM); San Antonio de Escazu, 1350 m, 2♀, 2♂ (MCZ). *Puntarenas:* Monteverde, ♀ (AMNH). PANAMA *Chiriquí:* Bambito, Volcán, ♀ (AMNH).

Araneus guatemus new species
Figures 211–214; Map 5

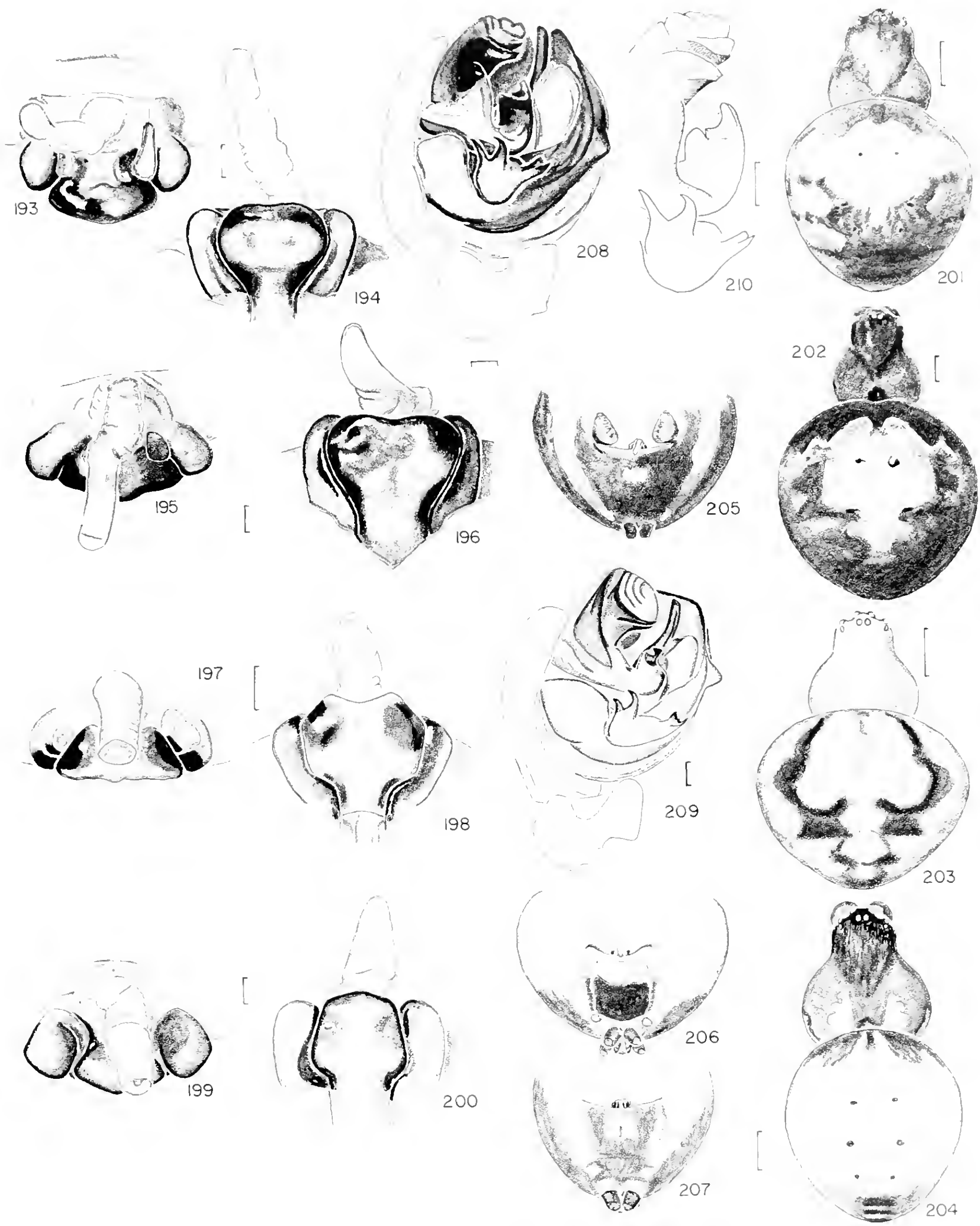
Neosconella styligera:—F. P.-Cambridge, 1904: 475, pl. 45, fig. 2, ♀. Female, paratype. (Not holotype of *styligera.*)

Holotype. Female from Guatemala in BMNH. The specific name is an arbitrary combination of letters.

Note. The specimen was on an insect pin in alcohol; the pin was carefully removed.

Description. Female holotype. Carapace grayish orange, sides of thorax olive. Chelicerae distally dark. Labium brown. Endites black. Sternum orange. Coxae, legs grayish orange. Dorsum of abdomen with a white T-shaped patch (Fig. 213); venter with white transverse patch behind epigynum followed by a dusky transverse patch in front of spinnerets; spinnerets brown (Fig. 214). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1.2 diameters apart, 1.5 from laterals. Posterior median eyes 0.8 diameter apart, 2.5 from laterals. Legs with relatively short macrosetae. Abdomen as long as wide, widest anteriorly. Total length 6 mm. Carapace 2.7 mm long, 2.2 wide. First femur 3.1 mm, patella and tibia 3.6, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.0 mm, third 1.7, fourth 2.6.

Diagnosis. The triangular scape (Fig. 211) distinguishes the species from *A. expletus* (Fig. 195).



Figures 193–210. *Araneus expletus* (O. P.-Cambridge). 193–207. Female. 193, 195, 197, 199. Epigynum, ventral. 194, 196, 198, 200. Epigynum, posterior. 201–204. Dorsal. 205–207. Abdomen, ventral. 208–210. Male, left palpus. 208, 209. Mesal. 210. Median apophysis, embolus, subterminal and terminal apophyses. 193, 194, 201 (type of *A. expletus,* Guatemala). 195, 196, 202, 205 (holotype of *A. smithi,* Veracruz, Mexico). 197, 198, 203, 206, 209 (Veracruz, Mexico). 199, 200, 204, 207 (Costa Rica). 208, 210 (holotype of *A. styligera,* Guatemala).

Scale lines. 1.0 mm, genitalia 0.1 mm.

Araneus rufipes (O. P.-Cambridge)
Figures 215–218; Map 3

Epeira rufipes O. P.-Cambridge, 1889: 31, pl. 4, fig. 12, ♀. Female holotype from Sabó, Vera Paz [Sabob, NE corner of Baja Verapaz, 6 km E of Parulhá, 970 m, 15°15′N, 90°09′W, Guatemala], in BMNH, examined.
Aranea rufipes:—F. P.-Cambridge, 1904: 515, pl. 49, fig. 17, ♀.
Aranea cambridgei Roewer, 1942: 838. New name for *Epeira rufipes* O. P.-Cambridge, thought preoccupied by *Aranea rufipes* Linn. (= *Gongylidium rufipes*).
Araneus rufipes:—Bonnet, 1955: 587.

Description. Female. Carapace dark brown, sides of thorax orange. Chelicerae dark brown. Sternum orange. Coxae light orange. Legs orange. Dorsum of abdomen white, without markings (Fig. 217); venter with white pigment patch behind epigynum, surrounded by dusky area; a pair of white spots in front of spinnerets; spinnerets brown (Fig. 218). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.3 diameters apart, 2 from laterals. Posterior median eyes 0.6 diameter apart, slightly more than 3 from laterals. Abdomen spherical. Total length 8.5 mm. Carapace 4.2 mm long, 3.2 wide. First femur 4.1 mm, patella and tibia 4.7, metatarsus 3.1, tarsus 1.2. Second patella and tibia 4.0 mm, third 2.7, fourth 3.8.

Diagnosis. Because of the unusual markings on the venter of the abdomen (Fig. 218), this species appears close to *A. pegnia* and *A. guatemus*. It differs from both these species by the nearly circular scape (Fig. 215).

Araneus habilis (O. P.-Cambridge)
Figures 219–222; Map 3

Epeira habilis O. P.-Cambridge, 1889: 28, pl. 8, fig. 3, ♀. Female syntypes from Chilascó Mts., Cobán, and Magdalena near Antigua, Guatemala, in BMNH, examined. Keyserling, 1892: 220, pl. 10, fig. 163, ♀.
Neosconella habilis:—F. P.-Cambridge, 1904: 477, pl. 45, fig. 8, ♀. Bonnet, 1958: 3061.
Aranea habilis:—Roewer, 1942: 844.

Note. In 1969, I made a sketch of specimens labeled *Neosconella habilis* from Chilascó and examined specimens from Cobán. In 1987, I examined and illustrated (Figs. 219–222) a specimen labeled, presumably by Pocock, "*Araneus hebilis* Keyserling: Type, Guatemala." This vial also contained a blue bordered Keyserling label, "*Epeira hebilis.*" All appear to be the same species.

Description. Female from Guatemala. Carapace dark orange. Sternum brown, coxae yellow. Legs dark orange, with indistinct darker rings on ends of tibiae and metatarsi. Dorsum of abdomen white, anterior and sides black (Fig. 221). Venter with pair of white spots behind epigynum (Fig. 222). Posterior median eyes same diameter as anterior medians, anterior lateral eyes 0.6 diameter, posterior laterals 0.8. Anterior medians 1.1 diameters apart, 1.2 from laterals. Posterior medians 0.3 diameter apart, 1.8 from laterals. Abdomen subspherical. Total length 5.8 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.9 mm, patella and tibia 3.5, metatarsus 2.5, tarsus 1.0. Second patella and tibia 2.9 mm, third 1.8, fourth 2.5.

Diagnosis. This species differs from related ones by having the lateral plates fused anteriorly at the origin of the scape, so they surround the median plate (Fig. 219).

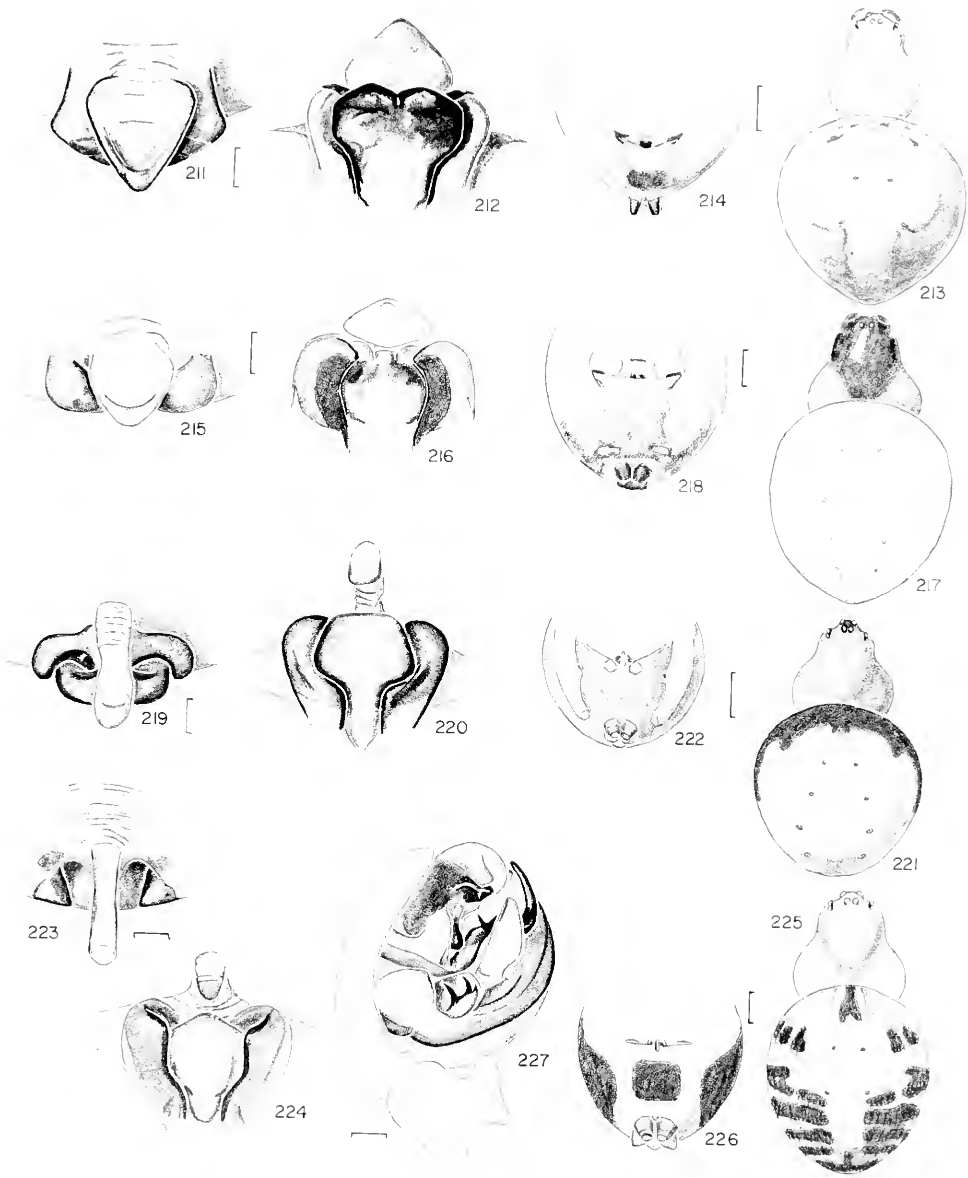
Distribution. Chiapas, Mexico, to Guatemala (Map 3).

Record. MEXICO *Chiapas:* Triunfo, 2000 m, Apr. 1942, ♀ (H. Wagner, AMNH).

Araneus galero new species
Figures 223–227; Map 3

Holotype. Female holotype, male and immature paratypes from Cerro Galero, Panamá Prov., Panama, July 1981 (W. Eberhard, no. 2222), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, sides of thorax lighter. Sternum and legs orange, leg four with distal half of tibia and metatarsus dark. Dorsum of abdomen with transverse black marks, which have more setae than light areas (Fig. 225). Venter with black square (Fig. 226). Posterior median and anterior lateral eyes 0.8 di-



Figures 211–214. *Araneus guatemus* n. sp., female. 211. Epigynum, ventral. 212. Epigynum, posterior. 213. Dorsal. 214. Abdomen, ventral.

Figures 215–218. *A. rufipes* (O. P.-Cambridge), female. 215. Epigynum, ventral. 216. Epigynum, posterior. 217. Dorsal. 218. Abdomen, ventral.

Figures 219–222. *A. habilis* (O. P.-Cambridge), female. 219. Epigynum, ventral. 220. Epigynum, posterior. 221. Dorsal. 222. Abdomen, ventral.

Figures 223–227. *A. galero* n. sp. 223–226. Female. 223. Epigynum, ventral. 224. Epigynum, posterior. 225. Dorsal. 226. Abdomen, ventral. 227. Male, left palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

ameter of anterior medians, posterior lateral eyes 0.7 diameter. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.7 diameter apart, a little over 2 from laterals. Abdomen broadly oval. Total length 9.2 mm. Carapace 4.7 mm long, 3.7 wide. First femur 5.5 mm, patella and tibia 6.1, metatarsus 4.0, tarsus 1.6. Second patella and tibia 5.4 mm, third 3.3, fourth 4.9.

Male. Head dark brown, brown continuing as a narrower band to posterior border of thorax, two brown patches on sides of orange thorax. Chelicerae dark brown. Sternum and coxae orange. First and second femur with distal ends and patellae dark brown. Abdomen colored as in female. Posterior median eyes 0.8 diameter of anterior medians, lateral eyes 0.7 diameter. Anterior median eyes their diameter apart, a little less than their diameter from laterals. Posterior median eyes 0.7 diameter apart, 1.7 from laterals. Endite with indistinct tooth. First coxa without hook. Second tibia same thickness as first. Abdomen subspherical. Total length 5.0 mm. Carapace 2.5 mm long, 2.1 wide. First femur 3.7 mm, patella and tibia 4.3, metatarsus 3.1, tarsus 1.2. Second patella and tibia 3.2 mm, third 1.8, fourth 2.7.

Variation. Total length of females 7.7 to 10.0 mm, of males 4.9 to 5.0. The small distal tooth in the median apophysis of the male's palpus may be absent.

Diagnosis. The female is distinguished from others by the shape of the epigynum and by having a hollow behind the scape in ventral view, flanked by a triangular sclerotized sclerite on each side (Fig. 223). The male is distinguished from that of *A. pegnia* (Fig. 234) by the curved embolus, its tip pointing to the conductor (Fig. 227). The cap on the embolus in Figure 227 is often absent.

Distribution. Panama to Colombia (Map 3).

Paratypes. PANAMA *Panamá:* Playa Corona nr. San Carlos, 8 Aug. 1983, ♀ (H., L. Levi, MCZ); nr. Arraiján, 18 July 1979, ♀ (M. Stowe, MCZ); Cerro Galero, 30 m, June 1985, ♂, imm. (W. Eberhard, no. 2843, MCZ); Cerro Galero, July 1981, ♂, July 1985, ♂, imm. (W. Eberhard, nos. 2843, 2863, MCZ); Barro Colorado Island, Aug. 1974, ♀, ♂ (W. Eberhard, no. 901, MCZ). COLOMBIA *Caquetá:* Río Orteguaza, 200 m, Aug.–Sept. 1947, ♀ (L. Richter, AMNH). PERU *Loreto:* Jenaro Herrera nr. Iquitos, 04°55′S, 73°45′W, ♀ (MHNSM).

Araneus pegnia (Walckenaer)
Figures 228–234; Map 3

Epeira pegnia Walckenaer, 1841: 80. Name for Abbot's Georgia Spiders manuscript, figs. 375, 389, 484. Copy of manuscript in MCZ, examined.

Epeira globosa Keyserling, 1865: 820, pl. 18, figs. 19. 20, ♀. Two female syntypes from New Granada in BMNH, examined.

Epeira solersioides O. P.-Cambridge, 1889: 25, pl. 7, fig. 15, ♂. Male holotype from Bugaba, Panama, in BMNH, examined.

Neosconella bella Chamberlin and Ivie, 1942: 78, figs. 223, 224, ♂. Male holotype from Laguna Beach, California, in AMNH.

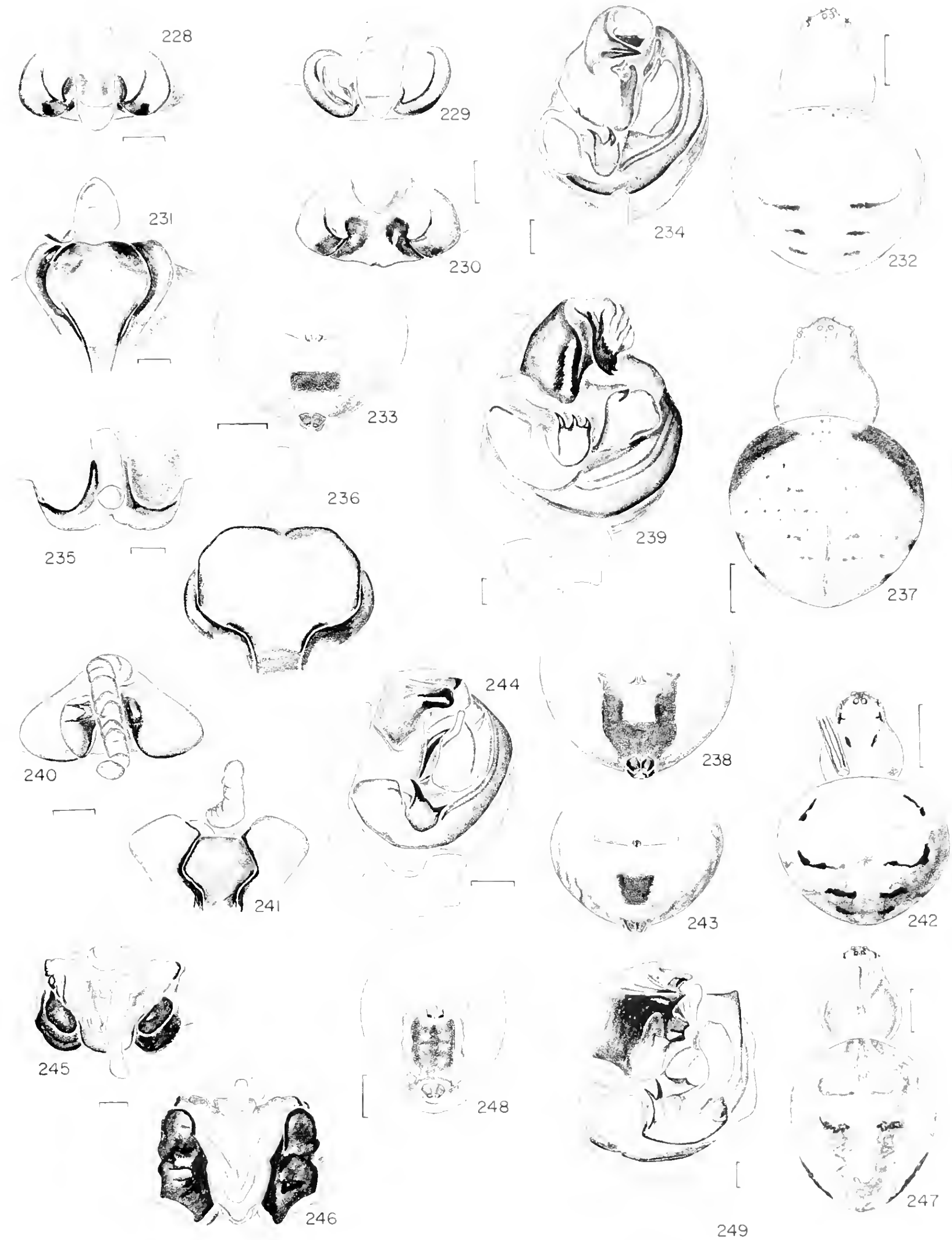
Araneus pegnia:—Levi, 1973: 546, figs. 426–428, ♀, ♂, map 6.

Description. Female from Panama. Carapace, sternum, legs orange. Dorsum of abdomen with four white patches, and three pairs of dusky transverse marks posteriorly (Fig. 232); venter with white patch posterior to epigynum, dusky behind (Fig. 233). Posterior median eyes same diameter as anterior medians, lateral eyes 0.8 diameter. Anterior median eyes a little more than their diameter apart, the same from laterals. Posterior median eyes 0.7 diameter apart, a little less than 2 from laterals. Abdomen oval, wider than long. Total

→

Figures 228–234. *Araneus pegnia* (Walckenaer). 228–233. Female. 228, 229. Epigynum, ventral. 230. Epigynum, ventroposterior. 231. Epigynum, posterior. 232. Dorsal. 233. Abdomen, ventral. 234. Male, left palpus.

Figures 235–239. *A. thaddeus* (Hentz). 235–236. Female. 235. Epigynum, ventral. 236. Epigynum, posterior. 237. Dorsal. 238. Abdomen, ventral. 239. Male palpus.



Figures 240–244. *A. lineatipes* (O. P.-Cambridge). 240–243. Female. 240. Epigynum, ventral. 241. Epigynum, posterior. 242. Dorsal, with first left femur. 243. Abdomen, ventral. 244. Male palpus.

Figures 245–249. *A. talca* n. sp. 245–248. Female. 245. Epigynum, ventral. 246. Epigynum, posterior. 247. Dorsal. 248. Abdomen, ventral. 249. Male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

length 5.4 mm. Carapace 2.3 mm long, 1.9 wide. First femur 2.7 mm, patella and tibia 3.1, metatarsus 2.1, tarsus 0.8. Second patella and tibia 2.5 mm, third 1.5, fourth 2.1.

Male from Panama. Carapace, coxae, and legs orange. Dorsum of abdomen with white pigment; venter orange-gray. Carapace high. Posterior median eyes same diameter as anterior medians, lateral eyes 0.8 diameter. Anterior median eyes their diameter apart, a little more than their diameter from laterals. Posterior median eyes 0.6 diameter apart, 1.4 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with macrosetae. Total length 3.3 mm. Carapace 1.8 mm long, 1.5 wide. First femur 2.5 mm, patella and tibia 2.9, metatarsus 1.8, tarsus 0.6. Second patella and tibia 1.9 mm, third 1.1, fourth 1.9.

Variation. Total length of females 3.5 to 6.3 mm, of males 2.5 to 4.3. The smallest specimens came from Jamaica. The shape of the notch on each side of the scape of the epigynum is variable.

Diagnosis. The female is distinguished by the notch on each side of the base of the epigynum (Figs. 228–230), the dark patches underneath the scape, and the rounded shape of the median plate in posterior view (Fig. 231). The male is distinguished by the two-clawed median apophysis (which often projects) and the slightly curved lateral edge of the embolus, with the tip of the embolus pointing toward the tip of the cymbium (Fig. 234).

Natural History. Specimens have been obtained with the Berlese funnel in Panama, sweeping roadside bushes in Oaxaca, on a forest path in Yucatan. Some Costa Rican specimens came from wasp nests.

Distribution. From Massachusetts and Indiana to Venezuela and coast of Ecuador, the Bahamas, Cuba, and Jamaica (Map 3).

Records from Mexico and the Neotropics. MEXICO *Tamaulipas:* 1.6 km N Gómez Farías (USNM). *Nuevo León:* 32 km W Linares, nr. León (CAS). *Baja California:* San Antonio (AMNH). *San Luis Potosí:* 10 km W San Joaquín (AMNH). *Durango:* Durango (AMNH); Rodeo (AMNH). *Jalisco:* hillside above Plan de Barrancas (AMNH); Barranca de Oblatos Guadalajara (AMNH). *Veracruz:* Jalapa (AMNH); Plan del Río (AMNH); Papantla (AMNH); Tuxpan (AMNH); Conejos (AMNH); Veracruz (AMNH). *Puebla:* Acatlán (AMNH); 7 km SW Acatepec (MCZ). *Morelos:* Cuernavaca (AMNH). *Guerrero:* Teloloapan, 1200 m (AMNH); Chilpancingo (AMNH). *Oaxaca:* Oaxaca, 1700 m (AMNH); Huajuapán (AMNH); Palomares (MCZ); 23 km SW Valle Nacional, Hwy. 175, 2600 m (MCZ); 17 km SW Valle Nacional, 650 m (MCZ). *Tabasco:* Teapa (BMNH). *Campeche:* Campeche (BMNH). *Yucatan:* Mérida (MCZ); Grutas de Loltan, 7 km S Oxkutzcab (MCZ); 12 km S Muna, Hwy. 261 (MCZ); Colonia Yucatan (AMNH); Uxmal (AMNH); Chichén Itzá (AMNH). *Chiapas:* Tuxtla Gutiérrez (AMNH); Chiapa (AMNH); Cintalapa (AMNH); Ocozocoautla (AMNH). GUATEMALA Tikal (MCZ). HONDURAS Tela (AMNH); Tsecucigaga, [?Tegucigalpa] (AMNH). EL SALVADOR Quezaltepeque (CAS). COSTA RICA *Alajuela:* El Higuito (MCZ). *Puntarenas:* Sirena (MCZ). *Guanacaste:* Palo Verde, Bagaces (MCZ); 8 km S Cañas (MZCR) PANAMA *Bocas del Toro:* Rio Changuinola (MCZ). *Colón:* Fort Sherman (MCZ). *Panamá:* Madden Dam forest (MCZ); Corozal (MCZ); Bella Vista (MCZ); Ancon (MCZ); Taboga Isl. (MCZ); Summit (MCZ); El Valle (MCZ); Exp. Gardens (MCZ); Isla Barro Colorado (MCZ); Fort Kobbe (MCZ); nr. Balboa (MCZ). *Coclé:* Aguadulce (MIUP).

BAHAMAS Whale Cay (CAS). South Bimini (AMNH). Grand Bahama Isl. (AMNH). Nassau (AMNH). CUBA *Pinar del Río:* Sierra de Anafe (AMNH); San Vicente (AMNH); Peninsula de Guananacabibes (AMNH). JAMAICA *St. Andrew:* Mona Rd. (MCZ). *St. Catherine:* Ewarton (MCZ); Rio Coore Gorge (MCZ).

VENEZUELA *Carabobo:* San Esteban

(AMNH). COLOMBIA *Magdalena:* Gaira, 10 m (MCZ); Sierra Nevada de Santa Marta (MCZ); San Pablo–San Pedro, 700 m (JAK). ECUADOR *Manabi:* Manta, ♂ (H. Exline, CAS). *Guayas:* Colonche, ♀ (H. Exline, CAS).

Araneus thaddeus (Hentz)
Figures 235–239; Map 3

Epeira thaddeus Hentz, 1847: 473, pl. 31, fig. 6, ♀. Female specimens from Alabama, destroyed.
Araneus thaddeus:—Levi, 1973: 544, figs. 415–425, ♀, ♂.

Note. The synonymy of *Epeira meropes* Keyserling with *thaddeus* (Levi, 1973) proved to be an error.

Description. Female from Mexico. Carapace orange-brown with white setae; sternum dark brown. Coxae light brown; legs orange and brown ringed. Dorsum of abdomen light brown, dark anteriorly on sides (Fig. 237); venter with wide black median band enclosing a square white patch behind epigynum (Fig. 238). Eyes subequal. Anterior median eyes 2 diameters apart, 2 from laterals. Posterior median eyes a little less than their diameter apart, a little more than 2 from laterals. Abdomen spherical, wider than long (Fig. 237). Total length 6.7 mm. Carapace 2.8 mm long, 2.3 wide. First femur 3.4 mm, patella and tibia 3.9, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.2 mm, third 1.9, fourth 2.7.

Male from Mexico. Coloration less distinct than that of female. Posterior median and lateral eyes 0.6 diameter of anterior median eyes. Anterior median eyes a little more than their diameter apart, the same from laterals. Posterior median eyes a little less than their diameter apart, 2.8 from laterals. Endite with tooth. First coxa with hook. Second tibia slightly thicker than first. Total length 5.2 mm. Carapace 2.8 mm long, 2.3 wide. First femur 4.7 mm, patella and tibia 5.3, metatarsus 3.8, tarsus 1.1. Second patella and tibia 3.9 mm, third 2.0, fourth 2.7.

Variation. Total length of Mexican females 6.2 to 7.9 mm, of males 4.3 to 5.2.

Diagnosis. Females can be separated from those of *A. pegnia* (Fig. 228) by the two concave borders of the median plate in ventral view (Fig. 235) and by the large, transverse, rectangular median plate in posterior view (Fig. 236). The male differs from others by the presence of three teeth on the median apophysis, and by the large terminal apophysis tipped by two small teeth (Fig. 239).

Natural History. Most records are from high elevations and one from a pine forest in the state of Mexico.

Distribution. Eastern United States, except Florida, scattered records from western United States to the Strait of Tehuantepec, Mexico.

Records from Mexico. Durango: 10 km NE El Salto, 11 Aug. 1947, ♂ (W. J. Gertsch, AMNH); 16 km E El Salto, 8 Aug. 1947, ♂ (W. J. Gertsch, AMNH). *México:* Oxtotilpan, ♀, ♂ (M. L. Jiménez, MCZ). *Distríto Federal:* Mexico City, 25 Sept. 1957, 3♀, ♂ (R. Dreisbach, MCZ); Santa Rosa, 24 July 1947, ♂ (H. Wagner, AMNH); W Río Frío, 2900 m, 22 Aug. 1964, 7♀, 5♂ (J., W. Ivie, AMNH); 16 km S Mexico City, 29 Nov. 1948, 3♀ (R. B. Fischer, AMNH); Desierto de los Leones, 4 Aug. 1946, ♂ (C. Goodnight, AMNH); Contreras, 14 Aug. 1946, ♀ (C. Goodnight, Bordas, AMNH). *Puebla:* 10 km E Río Frío, 22 Aug. 1964, ♀ (J., W. Ivie, AMNH). *Oaxaca:* on ridge E Cerro San Felipe, 2500–2700 m, 28 Sept. 1961, ♂ (C. M., M. R. Bogert, AMNH).

Araneus lineatipes (O. P.-Cambridge)
Figures 240–244; Map 3

Epeira lineatipes O. P.-Cambridge, 1889: 30, pl. 7, figs. 17, 18, ♀, ♂. Male and two female syntypes from road between Retalhuleu and Mazatenango, Santa Ana and Guatemala City, Guatemala, in BMNH, examined. Keyserling, 1892: 190, pl. 9, figs. 141, 142, ♀, ♂.
Neosconella lineatipes:—F. P.-Cambridge, 1904: 476, pl. 45, figs. 5, 6, ♀, ♂. Bonnet, 1958: 3062.
Aranea lineatipes:—Roewer, 1942: 846.

Description. Female from San Luis Potosí, Mexico. Carapace orange-yellow with black mark on each side of head. Sternum orange-yellow. Coxae orange-yellow, an-

terior two with black spot. Legs orange-yellow, first and second femur with three ventral black longitudinal lines on venter (Fig. 242). Dorsum of abdomen white anteriorly, black transverse bands posteriorly; venter with white spots posterior to epigynum, black anterior to spinnerets, white spot on each side slightly anterior to spinnerets (Fig. 243). Posterior median eyes 1.2 diameters of anterior medians, lateral eyes 0.8 diameter. Anterior medians a little more than their diameter apart, the same from laterals. Posterior medians 0.8 diameter apart, 1.2 from laterals. Abdomen oval (Fig. 242). Total length 3.0 mm. Carapace 1.4 mm long, 1.3 wide. First femur 1.7 mm, patella and tibia 2.0, metatarsus 1.2, tarsus 0.7. Second patella and tibia 1.6 mm, third 0.9, fourth 1.3.

Male from San Luis Potosí. Color as in female; leg lines less distinct. Posterior median eyes 0.8 diameter of anterior medians, lateral eyes 0.6 diameter. Anterior medians their diameter apart, 0.7 from laterals. Posterior medians 0.8 diameter apart, 1.5 from laterals. Endite with tooth. First coxa with hook. Second tibia swollen, with macrosetae; second femur with ventral row of macrosetae. Total length 2.7 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.7 mm, patella and tibia 2.0, metatarsus 1.3, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.9, fourth 1.2.

Variation. Total length of females 2.9 to 4.1 mm, of males 2.3 to 2.7.

Diagnosis. This small species is separated from all others by the distinct black lines on the venter of the femora of legs (Fig. 242). The epigynum has a notch in the base behind the narrow scape (Fig. 240). The male is separated from others by the round median apophysis with two spines, one pointing distally and one at right angles laterally (Fig. 244).

Natural History. Specimens have been collected from semi-desert scrub in Michoacan and short tropical rain forest in Campeche. All come from low elevations.

Distribution. Mexico to Honduras (Map 3).

Records. MEXICO *San Luis Potosí:* Valles (AMNH); Tamazunchale (AMNH). *Nayarit:* 8 km E, 6.5 S San Blas (WS); San Blas (AMNH); Tepic (AMNH). *Colima:* Las Humedades, Armeriá (AMNH). *Michoacan:* Apatzingzán, 400 m (MCZ). *Guerrero:* Acamixtla (AMNH); Acapulco (MCZ). *Oaxaca:* Puerto Escondido (MCZ); Tehuantepec (AMNH); 3 km SE Niltepec (AMNH); Puerto Escondido (MCZ). *Campeche:* Chicanna ruins, ca. 8 km W Xpujil (MCZ). *Chiapas:* 5 km NE Los Amates at Hwy. 190 (REL); Cintalapa (AMNH); Ocosingo, 900 m (AMNH); El Real (AMNH). GUATEMALA Ayutla (AMNH); Rabinal (AMNH); Los Ramones (AMNH). HONDURAS Copán (AMNH.)

Araneus talca new species
Figures 245–249; Map 3

Holotype. Female holotype, and three female and four male paratypes from Alto de Vilches, Andes montains, Talca Prov., Chile, 17–24 Oct. 1964 (L. Peña), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-yellow, head darker and with white setae, sides of carapace with a darker band. Chelicerae orange-yellow. Labium, endites, sternum brown. Coxae, legs dusky yellow, lightest proximally, darkest distally. Dorsum of abdomen with black spots forming an indistinct folium, sides darker gray with a white border toward the dorsum (Fig. 247); venter black between epigynum and spinnerets with a white line on each side and a white spot on the sides anterior of the spinnerets (Fig. 248). Posterior median eyes 1.3 diameters of anterior medians, laterals 1.1 diameters. Anterior median eyes slightly less than 2 diameters apart, the same from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen elongate oval (Fig. 247). Total length 5.8 mm. Carapace 2.3 mm long, 1.9 wide. First femur 2.4 mm, patella and tibia 3.1, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.5 mm, third 1.5; fourth 2.2.

Male. Color as in female, except ster-

num lighter and abdominal pattern more distinct. Posterior median eyes 1.3 diameters of anterior medians, laterals 1.1 diameters. Anterior median eyes slightly more than their diameter apart, 1.2 from laterals. Posterior median eyes their diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first, with macrosetae. Abdomen oval. Total length 4.4 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.1 mm, patella and tibia 2.7, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.1 mm, third 1.2, fourth 1.8.

Variation. Total length of females 5.1 to 7.4 mm, of males 4.4 to 5.2. The female commonly has a dorsal median white line on the abdomen, but always has a dark patch bordered by white posteriorly on each side (Fig. 247).

Diagnosis. Females can be separated from other *Araneus* species by the lobes of the sclerotized lateral plates, which are visible posteriorly on each side of the triangular base of the epigynum (Fig. 245). The male differs from *A. concepcion* (Fig. 253) by having the two spines of the median apophysis on a long neck (Fig. 249).

Distribution. Neuquén, Chubut Provinces, Argentina and Chile in Andes (Map 3). The northernmost Chilean localities may be mislabeled in the vial.

Natural History. One collection from Concepción is marked "edge of field."

Paratypes. ARGENTINA *Neuquén:* Pucará (MACN); Lago Lacar E Huahun (ZMK). *Río Negro:* El Bolsón (AMNH). *Chubut:* Lago Puelo (AMNH). CHILE *Antofagasta:* Antofagasta (IRSNB); E Taltal, 600 m (AMNH). *Coquimbo:* El Bato, E Illapel (AMNH). *Valparaíso:* Quebr. de Córdoba, El Tabo (AMNH); Valparaíso (MCZ). *Santiago:* Q. Córdoba (AMNH); Las Cruces Parral (IRSNB); Pirque (AMNH); Quilicura (AMNH); Piche Alhué (MCZ); Santiago (AMNH). *O'Higgins:* Pilay, 800 m (AMNH). *Curicó:* Las Tablas E Curicó (AMNH); E Curicó (AMNH). *Linares:* Fundo Malcho Andes in Parral (MCZ). *Ñuble:* Recinto Chillan area, 1000 m (AMNH). *Concepción:* Concepción (AMNH); Bosque Ramuntcho (AMNH); Hualpen, 60 m (AMNH). *Bío-Bío:* El Manzano nr. Contulmo (AMNH); Angol (CAS). *Malleco:* Curacautín (AMNH); 20 km E Temuco (CAS); Malalcahuello (AMNH). *Cautín:* 30 km NE Villarrica (MCZ); Toltén (AMNH). *Valdivia:* Puyehue, 600 m (AMNH); NW Panguipulli (AMNH). *Osorno:* Pucatrihue (AMNH); Purranque (AMNH); Anticura nr. Puyehue (AMNH). *Llanquihue:* Correntoso (MCZ). *Chiloé:* Río Ventisquero, Lago Velcho (AMNH). [?]: Los Muermos Forest (CAS).

Araneus concepcion new species
Figures 250–253; Map 3

Holotype. Female holotype and two female paratypes from Bosque de Ramuntcho, Concepción Prov., Chile, 12–13 Dec. 1963 (A. F. Archer), in AMNH, one paratype in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, head slightly dusky. Chelicerae, labium, endites orange. Sternum orange. Coxae orange; legs orange, distal articles dusky, indistinctly ringed. Dorsum of abdomen spotted without distinct pattern (Fig. 252); venter dusky-gray between epigynum and including spinnerets, a white line on each side of dusky patch. Posterior median and anterior lateral eyes 1.3 diameters of anterior medians, posterior laterals 1 diameter. Anterior median eyes slightly less than 2 diameters apart, 2 from laterals. Posterior median eyes 0.7 their diameter apart, 2.5 from laterals. Abdomen as wide as long, subtriangular, with humps indistinct (Fig. 252). Total length 6.0 mm. Carapace 2.8 mm long, 2.2 wide. First femur 2.8 mm, patella and tibia 3.5, metatarsus 2.1, tarsus 0.8. Second patella and tibia 3.0 mm, third 1.7, fourth 2.7.

Male from type locality. Color as in female. Eyes subequal. Anterior median eyes 1.2 diameters apart, 1.2 from laterals. Posterior median eyes 0.8 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first,

with some macrosetae. Abdomen oval, wider in front than behind. Total length 4.2 mm. Carapace 2.3 mm long, 2.1 wide. First femur 2.7 mm, patella and tibia 3.5, metatarsus 1.9, tarsus 0.7. Second patella and tibia 2.6 mm, third 1.6, fourth 2.2.

Variation. Total length of females 6.0 to 6.9 mm.

Diagnosis. The female differs from *A. zapallar* (Figs. 254, 255) by having a longer base (Fig. 250) and larger lateral plates in posterior view (Fig. 251). The proximal biforked end of the median apophysis of the male's palpus has a shorter neck (Fig. 253) than that of *A. talca* (Fig. 249).

Paratypes. CHILE *Coquimbo:* 5 km N Los Vilos, 5 Jan. 1985, ♂ (N. Platnick, O. Francke, AMNH). *Valparaíso:* central coast, 31 Oct. 1982, ♂ (AMNH). *Ñuble:* Cobquecura Tregualemu, 31 Dec. 1958, 2♀ (L. Peña, IRSNB). *Concepción:* Bosque Remuntcho, 12–13 Dec. 1961, 3♀, 2♂ (A. F. Archer, AMNH).

Araneus zapallar new species
Figures 254–257; Map 3

Holotype. Female holotype and female paratype from Valparaiso, Valparaiso Prov., Chile, 22 Dec. 1972 (W. C. Sedgwick), in MCZ. The specific name is a noun in apposition after the locality of a paratype.

Description. Female paratype from Zapallar. Carapace orange with short white setae, thorax underlain by two white pigment patches in center. Chelicerae orange. Labium, endites dark orange. Sternum orange underlain with white pigment spots. Coxae orange; legs orange with indistinct darker rings on last legs. Dorsum of abdomen with transverse dusky stripes and one white transverse band (Fig. 256); venter with whitish square, lightest around margin, and two white spots on each side of spinnerets (Fig. 257). Posterior median eyes 1.3 diameters of anterior medians, laterals 1.1 diameters. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen slightly longer than wide, with rounded lateral humps (Fig. 256). Total length 5.3 mm. Carapace 2.1 mm long, 1.8 wide. First femur 2.1 mm, patella and tibia 2.6, metatarsus 1.6, tarsus 0.7. Second patella and tibia 2.1 mm, third 1.3, fourth 1.9.

Variation. Total length of females 5.0 to 7.0 mm.

Diagnosis. This species differs from *A. concepcion* (Figs. 250, 251) by having a shorter base (Fig. 254) and smaller lateral plates. The median depression of the median plate is wider than long in posterior view (Fig. 255).

Paratypes. CHILE *Coquimbo:* 5 km N Los Vilos, 5 Jan. 1985, ♀ (N. Platnick, O. Francke, AMNH). *Aconcagua:* Zapallar, 27 Nov. 1950, 2♀ (E. S. Ross, A. E. Michelbacher, CAS); Los Molles, 2 m, 9 Jan. 1985, ♀ (N. Platnick, O. Francke, AMNH). *Valparaíso:* central coast, 31 Oct. 1982, ♀ (L. Peña, AMNH); Valparaíso, 22 Dec.

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Figures 250–253. *Araneus concepcion* n. sp. 250–252. Female. 250. Epigynum, ventral. 251. Epigynum, posterior. 252. Dorsal. 253. Male, left palpus.

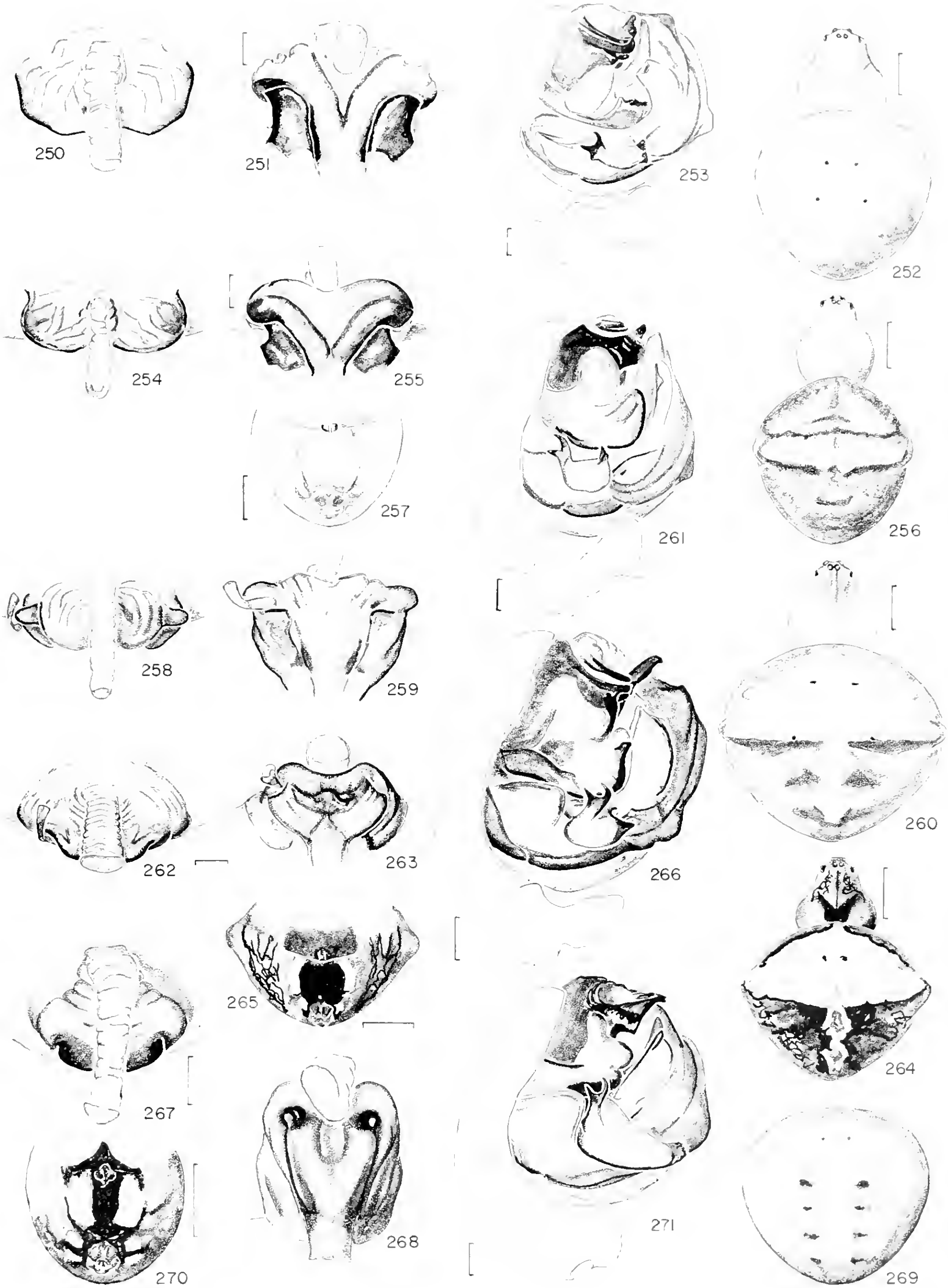
Figures 254–257. *A. zapallar* n. sp., female. 254. Epigynum, ventral. 255. Epigynum, posterior. 256. Dorsal. 257. Abdomen, ventral.

Figures 258–261. *A. huahun* n. sp. 258–260. Female. 258. Epigynum, ventral. 259. Epigynum, posterior. 260. Dorsal. 261. Male palpus.

Figures 262–266. *A. alhue* n. sp. 262–265. Female. 262. Epigynum, ventral. 263. Epigynum, posterior. 264. Dorsal. 265. Abdomen, ventral. 266. Male palpus.

Figures 267–271. *A. titirus* Simon. 267–270. Female. 267. Epigynum, ventral. 268. Epigynum, posterior. 269. Abdomen, dorsal. 270. Abdomen, ventral. 271. Male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.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1972, ♀ (W. C. Sedgwick, MCZ); Bosque Quintero, 20 Feb. 1973, ♀ (L. Cartagena, MCZ). *Santiago:* Quebrada Córdoba Coast, 15–20 Feb. 1979, 2♀ (L. Peña, AMNH).

Araneus huahun new species
Figures 258–261; Map 3

Holotype. Female holotype from Huahun, Neuquén, Argentina, 17 Jan. 1985 (E. Maury), in MACN. The specific name is a noun in apposition after the type locality, spelled as above (there are various spellings of the type locality).

Description. Female holotype. Carapace yellowish with head dusky. Chelicerae yellowish. Labium, endites dusky. Sternum dark dusky. Coxae yellowish; legs yellowish with indistinct, wide, darker rings. Dorsum of abdomen with transverse dusky and white marks (Fig. 260); venter with a dusky area in middle, framed by a white line on each side and a white spot on each side anterior of spinnerets; spinnerets dusky. Posterior median eyes 1.2 diameters of anterior medians, anterior laterals 1 diameter, posterior laterals 0.8. Anterior median eyes slightly more than 1 diameter apart, 1.5 from laterals. Posterior median eyes 0.7 their diameter apart, slightly more than 2 from laterals. Abdomen subspherical with distinct humps (Fig. 260). Total length 6.5 mm. Carapace 2.5 mm long, 2.1 wide. First femur 2.5 mm, patella and tibia 3.1, metatarsus 1.9, tarsus 0.7. Second patella and tibia 2.5 mm, third 1.5, fourth 2.3.

Male from Santiago Prov., Chile. Color as in female. Posterior median eyes same diameter as anterior medians, anterior laterals 1 diameter, posterior laterals 0.7. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes 1.3 diameters apart, 2.5 from laterals. Endite with tooth dorsal in position. First coxa with hook. Second tibia thicker than first, with short anterior macrosetae. Abdomen oval, slightly longer than wide, widest in front. Total length 3.7 mm. Carapace 1.9 mm long, 1.6 wide. First femur 2.2 mm, patella and tibia 2.6, metatarsus 1.6, tarsus 0.5. Second patella and tibia 2.1 mm, third 1.3, fourth 1.7.

Variation. Total length of females 4.4 to 6.5 mm, of males 3.2 to 3.8.

Diagnosis. Females differ from those of *A. alhue* (Figs. 262, 263) by having a transverse sclerotized fold on each side of the epigynum base in ventral view (Fig. 258) and having the lateral plates in posterior view with a 90° angle toward the median (Fig. 259). Males differ from *A. alhue* (Fig. 266) by having the embolus rounded laterally, the tip pointing toward the cymbium, and the embolus lamella long and the terminal apophysis projecting (Fig. 261).

Natural History. Specimens have been collected in montane forest in Talca Province, and in *Nothofagus* forest in Ñuble and Talca.

Distribution. Neuquén and Chubut Provinces of Argentina, and Chile (Map 3).

Paratypes. ARGENTINA *Neuquén:* S. Martín de los Andes; El Venado (both MACN). *Río Negro:* Bariloche (MACN). *Chubut:* Cholila (MACN). CHILE *Coquimbo:* 3 km E El Tofo; 15 km SW Ovalle; Pta. Teatinos N. de La Serena; Los Vilos (all AMNH). *Aconcagua:* El Injenio, La Ligua (MCZ). *Valparaíso:* Cuesta El Melón (AMNH); Olmué (AMNH); Quillota (AMNH); Viña del Mar (AMNH); La Cruz (MCZ); Playa El Canelillo (MCZ). *Santiago:* Ojesta Barrlyn (MCZ); Tiltil, 800–1300 m; Prique; S Melipilla; Santiago (all AMNH). *Curicó:* E Curicó (AMNH). *Talca:* 70 km E Talca, Alto de Vilches (AMNH). *Ñuble:* rd. to Pemuco; 60 km SE Chillán, 1300 m; Chillán, Las Trancas (all AMNH). *Bío-Bío:* El Abanico (CAS); Trolguaca (IRSNB). *Malleco:* Cord. Chillán Las Cabras (IRSNB); Laguna Malleco (AMNH); Malalcahuello (AMNH); Tolhuaca (AMNH). *Cautín:* Chacano, NW Nueva Imperial (AMNH).

Araneus alhue new species
Figures 262–266; Map 3

Holotype. Female holotype from Piche, Alhué, Santiago Prov., Chile, 22 Nov. 1959 (L. Peña), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace dark brown, with black marks (Fig. 264). Chelicerae orange, proximally black. Labium, endites dark brown. Sternum dark brown. Coxae yellowish; legs orange, ringed blackish-brown. Dorsum of abdomen with white anterior semicircle and posterior median longitudinal light band on black (Fig. 264); venter black bordered on each side by a white line, a reticulated pattern on each side (Fig. 265). Posterior median eyes 1.5 diameters of anterior medians, anterior laterals 1.3 diameters, posterior laterals 1. Anterior median eyes 1.4 diameters apart, 1.3 from laterals. Posterior median eyes their diameter apart, 1.8 from laterals. Abdomen slightly wider than long, with rounded lateral humps (Fig. 264). Total length 4.5 mm. Carapace 1.7 mm long, 1.5 wide. First femur 1.9 mm, patella and tibia 2.3, metatarsus 1.5, tarsus 0.7. Second patella and tibia 1.9 mm, third 1.2, fourth 1.8.

Male. Color as in female. Posterior median eyes 1 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.2 diameters apart, 1.2 from laterals. Posterior median eyes 1 diameter apart, 2 from laterals. Endites with tooth. First coxa with hook. Second tibia thicker than first. Abdomen oval. Total length 3.5 mm. Carapace 1.8 mm long, 1.4 wide. First femur 2.0 mm, patella and tibia 2.5, metatarsus 1.3, tarsus 0.5. Second patella and tibia 1.9 mm; third 1.1, fourth 1.4.

Variation. Total length of females 3.6 to 5.6 mm, of males 3.2 to 3.8.

Diagnosis. Females are separated from other Chilean species by the hexagonal posterior median plate of the epigynum (Fig. 263); males by the projecting spur of the terminal apophysis and the laterally rounded embolus (Fig. 266). The median apophysis has a blunt point laterally (Fig. 266).

Distribution. Neuquén, Argentina, and Chile (Map 3).

Records. ARGENTINA *Neuquén:* Lago Lacar, 750 m (ZMK). CHILE *Coquimbo:* E Illapel (AMNH). *Aconcagua:* 10 km E Zapudo (CAS); Zapallar (CAS); region de Valparaíso, Petorca (AMNH). *Valparaíso:* Valparaíso (AMNH); nr. El Tabo Quintero (AMNH). *Santiago:* Pirque (AMNH); Cerro San Cristóbal, nr. Santiago City, 500–800 m (AMNH); N of Tiltil, 800–1300 m (AMNH); Las Cañas (AMNH); S Melipilla (AMNH). *Curicó:* Las Tablas, E Curicó (AMNH). *Ñuble:* SE Chillán, 800 m (AMNH); Las Trancas, Chillán (AMNH); 50 km E San Carlos (AMNH); 40 km E San Carlos (AMNH). *Concepción:* Pichinhue Cord. Nahuelbuta (IRSNB); 6 km S San Pedro, 360 m (AMNH). *Bío-Bío:* Caledonia, E Mulchen, 700–900 m (AMNH); nr. Contulmo (AMNH). *Malleco:* Caracautín (AMNH). *Cautín:* NW Nueva Imperial, W Temuco (AMNH). *Valdivia:* Purulón (AMNH).

Araneus titirus Simon
Figures 267–271; Map 3

Araneus titirus Simon, 1896: 67. Two female syntypes from Sierra de Chillán, Chillán, Chile, in MNHN no. 17692, examined. Bonnet, 1955: 613.
Aranea titira:—Roewer, 1942: 854.

Description. Female syntype. Carapace yellow-brown, center with some white pigment, sides brownish. Sternum black. Coxae yellowish white; legs yellow-white with thin line. Dorsum of abdomen spotted, light anteriorly with pairs of indistinct marks posteriorly (Fig. 269); venter black with white patch on each side and two small white spots on each side of spinnerets (Fig. 270). Eyes subequal. Anterior median eyes 1.7 diameters apart, 1.7 from laterals. Posterior median eyes 1.5 their diameter apart, 3 from laterals. Abdomen oval, wider than long, smooth (Fig. 269). Total length 3.6 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.6 mm, patella and tibia 1.8, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.9, fourth 1.3.

Male from Chubut Prov., Argentina. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1.3 diameters apart, 1.3 from laterals. Posterior median eyes 1.2 diameters apart, 2.5 from laterals. Endite

with tooth dorsal in position. First coxa with hook. Second tibia thicker than first with some anterior macrosetae. Abdomen oval. Total length 4.6 mm. Carapace 2.1 mm long, 1.8 wide. First femur 2.3 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 0.5. Second patella and tibia 2.0 mm, third 1.2, fourth 1.7.

Variation. Total length of females 3.6 to 6.4 mm, of males 3.5 to 4.6. The black venter of the abdomen with contrasting white streaks is barely visible in some specimens.

Diagnosis. When present, the white ventral streaks of the abdomen are diagnostic. The median plate of the epigynum in posterior view is longer than that of related species and has an interior depression (Fig. 268). The median apophysis of the male palpus differs from that of other species by being bulky and expanded underneath the neck with the two teeth, and by the terminal apophysis pointing laterally (Fig. 271). The embolus is hidden by two lobes of the distal hematodocha (Fig. 271).

Distribution. Neuquén and Río Negro Provinces of Argentina, and Chile (Map 3).

Records. ARGENTINA *Neuquén:* Huahum (MACN); Lagunas El Venada (MACN); Lago Guilléa (MACN); Nuhual Huapi (MACN); L. Lacar-Pucará (MACN); Pucará (MACN); Lago Lacar, Pucará, 750 m (ZMK). *Río Negro:* El Bolsón (AMNH); Río Azul (AMNH); Bariloche (ZMK). *Chubut:* Cholila, Lago Lezama (AMNH); Epuyén (AMNH); Lago Escondido (AMNH). CHILE *Coquimbo:* Cerro Talinay (AMNH), Nague (AMNH). *Aconcagua:* Zapallar (CAS). *Valparaíso:* nr. El Tabo (AMNH); Valparaíso (MCZ). *Santiago:* Malleco (AMNH); Quebrada Córdoba (AMNH). *Talca:* Alto de Vilches Andes (MCZ). *Linares:* Las Cruces Parral (IRSNB). *Ñuble:* Chillán (AMNH); Los Lleuques (AMNH); Cobquecura (IRSNB); Cord. Chillán, Las Cabras (IRSNB). *Concepción:* Pichinahué, Cord. Nahuelbuta (IRSNB). *Arauco:* Contulmo (MCZ). *Bío-Bío:* Trolguaca (IRSNB). *Malleco:* Las Raíces, 1200 m (AMNH); Curacautín (AMNH); Nahuelbuta Natl. Pk., 1300 m (AMNH); Malalcahuello, Region Araucania (AMNH); *Cautín:* NW Nueva Imperial (AMNH). *Valdivia:* Valdivia (MCZ, AMNH); central coast (AMNH). *Osorno:* Pucatrihue Coast (MCZ); Maullín (MNRJ). *Llanquihue:* Correntoso (MCZ). *Chiloé:* Dalcahue (MCZ). *Aysén:* Region Aysén del General Carloz Ibanez del Campo Bandurrias (AMNH); Aysén, Coihaique (IRSNB).

Araneus uniformis (Keyserling)
Figures 272–275; Map 3

Epeira uniformis Keyserling, 1880; 307, pl. 4, fig. 10, ♀. Female holotype from Neu Freiburg [Novo Friburgo, Rio de Janeiro], Brazil, in BMNH, examined. Keyserling, 1892: 160, pl. 8, fig. 118, ♀.

Epeira lucida Keyserling, 1884: 650, pl. 21, fig. 2, ♀. Female holotype from Santa Isabela, Rio Grande do Sul, Brazil, in NMI, examined. Keyserling, 1892: 126, pl. 6, fig. 93, ♀. NEW SYNONYMY.

Araneus candidus Simon, 1895: 809. Female lectotype, male paralectotype here designated from southern Brazil in MNHN no. 9726, examined. Bonnet, 1955:451. NEW SYNONYMY.

Aranea vespae Strand, 1908: 3. Five early instar syntypes from Joinvile, Santa Catarina, Brazil, in SMF, examined. Roewer, 1942: 856. NEW SYNONYMY.

Aranea candida:—Roewer, 1942: 838.

Aranea lucida:—Roewer, 1942: 846.

Aranea uniformis:—Roewer, 1942: 855.

Araneus candidus:—Bonnet, 1955: 451.

Araneus lucidus:—Bonnet, 1955: 530.

Araneus uniformis:—Bonnet, 1955: 626.

Araneus vespae:—Bonnet, 1955: 629.

Notes. Two females of *Epeira lucida* are in the National Museum of Ireland collection. One is the specimen Keyserling de-

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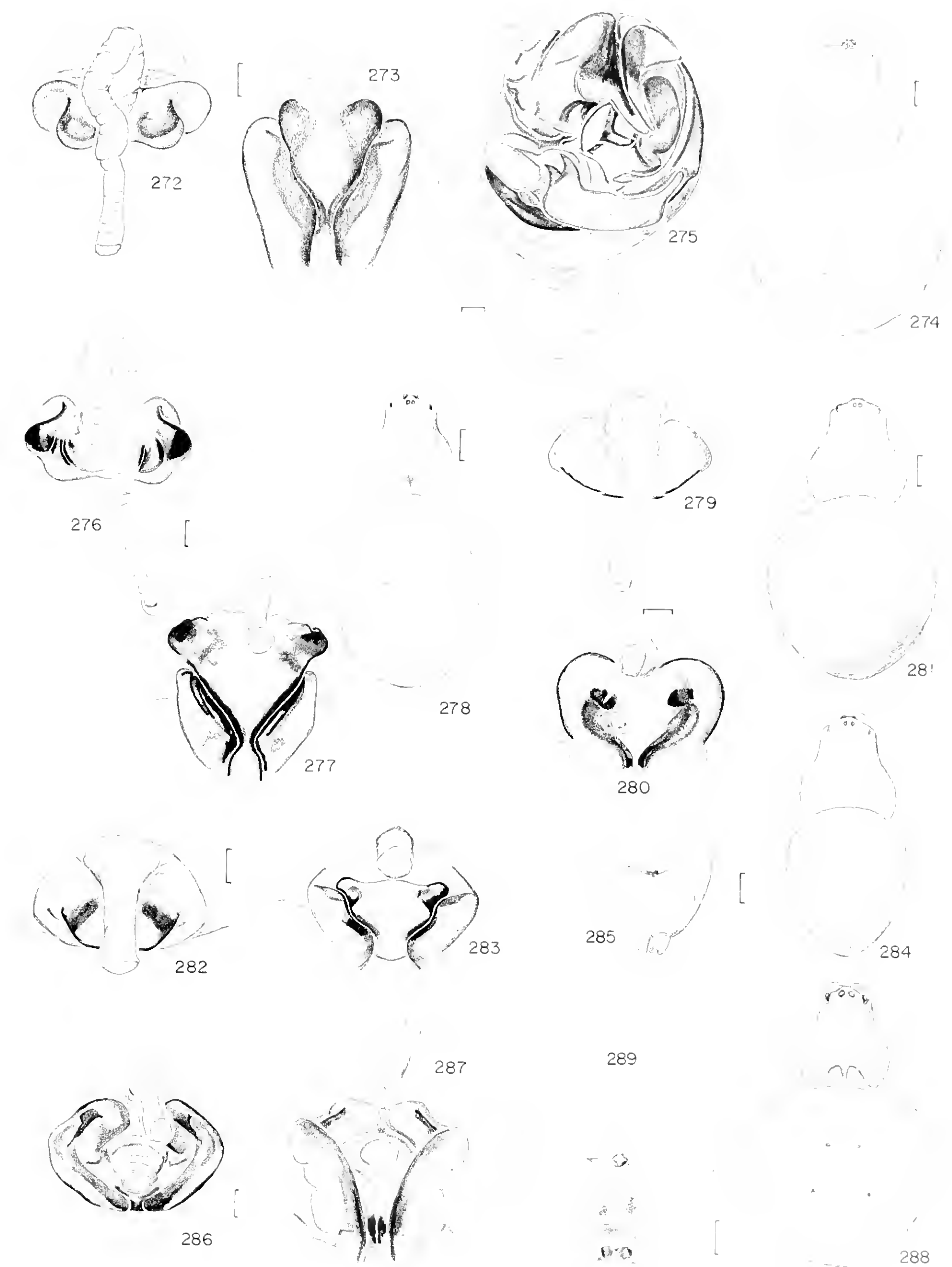
Figures 272–275 *Araneus uniformis* (Keyserling). 272–274. Female. 272. Epigynum, ventral. 273. Epigynum, posterior. 274. Dorsal. 275. Male, left palpus.

Figures 276–278 *A. cuiaba* n. sp., female. 276. Epigynum, ventral. 277. Epigynum, posterior. 278. Dorsal.



Figures 279–281. *A. villa*, n. sp., female. 279. Epigynum, ventral. 280. Epigynum, posterior. 281. Dorsal.

Figures 282–285. *A. concoloratus* (O. P.-Cambridge), female. 282. Epigynum, ventral. 283. Epigynum, posterior. 284. Dorsal. 285. Abdomen, ventral.

Figures 286–289. *A. sicki*, n. sp., female. 286. Epigynum, ventral. 287. Epigynum, posterior. 288. Dorsal. 289. Abdomen, ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.

scribed; the other is *Araneus workmani*. The one fitting the Keyserling description has been designated the holotype.

The label in the vial of *A. candidus* indicates numerous localities from Rio de Janeiro, Brazil, to Paraguay.

Strand writes that *A. vespae* differs from *A. lucida* by being green, smaller, and having a longer first metatarsus. It is smaller, and has a longer metatarsus because it is an early instar, and is green because it was more recently collected and is in better condition than other specimens of this species examined by Strand.

Description. Female from Pinhal, Est. Santa Catarina. Carapace, sternum, legs yellow, abdomen whitish (Fig. 274). Anterior median eyes slightly larger than others, laterals about 0.7 diameter of anterior medians. Anterior median eyes more than 1 diameter apart, posterior medians 1 diameter apart. Tarsi and metatarsi of legs 1 to 3 with prolateral fields of macrosetae. Total length 9.3 mm. Carapace 3.5 mm long, 2.9 wide. First femur 3.6 mm, patella and tibia 5.4, metatarsus 3.7, tarsus 1.3. Second patella and tibia 4.7 mm, third 2.7, fourth 3.7.

Male from Pinhal, Est. Santa Catarina. Coloration as in female. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5. Anterior medians their diameter apart, 1.8 from laterals. Posterior medians 0.7 their diameter apart, 4.2 from laterals. Endite with tooth. First coxa with hook. Second coxa with a proximal, light-colored, small tubercle. Second tibia thicker than first. Abdomen oval. Total length 6.3 mm. Carapace 3.4 mm long, 2.5 wide. First femur 3.4 mm, patella and tibia 5.2, metatarsus 3.4, tarsus 1.2. Second patella and tibia 4.6 mm, third 2.4, fourth 3.4

Variation. Living specimens, both male and female, are green (Kochalka, personal communication). The type of *A. lucidus* is only 6 mm total length, carapace 2.2 long. That of *A. candidus* is 12.7 mm total length, carapace 5.7 long. These are the extremes of the total length of females; total length of other females in collections 6.3 to 12.0 mm, of males 5.2 to 7.7.

Diagnosis. This species and the related *A. concoloratus* and *A. cuiaba* have small eyes. *Araneus uniformis* females are distinguished from those of *concoloratus* (Fig. 282) by the longer scape of the epigynum (Fig. 272) and from *A. cuiaba* (Fig. 277) by having the posterior median plate longer than wide (Fig. 273). Males differ from other known males by having a prong at the lateral end of the median apophysis and by the mushroom-shaped embolus, offset and lying on its side (Fig. 275).

Distribution. Southeastern Brazil to Argentina and Bolivia (Map 3).

Records. BRAZIL *Espírito Santo:* M. Moscoso, Vitória (MNRJ). *Minas Gerais:* Serra do Caraça (MZSP). *Rio de Janeiro:* Niterói (MNRJ); Poço Grande (MNRJ); Itatiaia (MNRJ); Petrópolis (AMNH). *São Paulo:* Barueri (MZSP); Itu (AMNH); Piraçununga (MZSP); Pôrto Cabral (MZSP); Mogi das Cruzes (MZSP). *Paraná:* Rolândia (AMNH); Rio do Malo (MNRJ). *Santa Catarina:* Blumenau (MZSP); Pinhal, 700 m (AMNH). *Rio Grande do Sul:* Porto Alegre (MNRJ); Santa Rosa (MCZ); Igrejinha (Jaguara) (MZSP); Montenegro (MCN); Canela (MCN); São Valentim (MCN); Capivari, Viamão (MCN); Triunfo (MCN); Quaraí (MCN); Estac. Ecológica de Taim, Rio Grande (MCN). URUGUAY *Tacuarembó:* Arroyo Laureles (MHNM). PARAGUAY *Concepción:* Fonciere (MCZ). *Chaco:* Madrejón (IBNP). BOLIVIA *La Paz:* Coroico, Yungas, 1600 m (IRSNB). ARGENTINA *Misiones:* Eldorado (AMNH); San Antonio (MACN); Pt. Rico (MACN). *Corrientes:* Paso de la Patria (MACN). *Chaco:* Sáenz Peña (MACN). *Catamarca:* Frías (CAS). *Córdoba:* 8 km N Deán Funes (CAS). *Buenos Aires:* Paraná de las Palmas (MEG); La Plata (MNRJ, MLP); Isla Flora, Tigre (MNRJ).

Araneus cuiaba new species

Figures 276–278; Map 3

Holotype. Female holotype from Cuiabá, Mato Grosso, Brazil, Nov. 1963 (M. Alvarenga), in AMNH.

The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange. Chelicerae, labium, endites, and sternum orange. Coxae, legs orange. Dorsum of abdomen lighter orange (Fig. 278); venter with white square between epigynum and spinnerets. Eyes small. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1.5 diameters apart, 2.5 from laterals. Posterior median eyes slightly less than their diameter apart, 3.5 from laterals. Sides and undersides of distal articles, especially of first two pairs of legs, with short macrosetae and setae. Abdomen elongate oval (Fig. 278). Total length 9.5 mm. Carapace 3.8 mm long, 2.8 wide. First femur 3.9 mm, patella and tibia 5.2, metatarsus 3.9, tarsus 1.2. Second patella and tibia 4.7 mm, third 2.6, fourth 4.1.

Diagnosis. This species differs from *A. uniformis* (Fig. 273) in that the lobes of the median plate overlap the lateral ones in ventral view (Fig. 276), and the median plate is as wide as long in posterior view (Fig. 277).

Paratypes. BRAZIL *Mato Grosso do Sul:* Corumbá, 28, 29 May 1960, 2♀ (B. Malkin, AMNH). ARGENTINA *Formosa:* Pt. Santos [?], ♀ (H. Hepper, MACN).

Araneus villa new species
Figures 279–281; Map 3

Holotype. Female holotype and one female paratype from Puente Villa, Yungas, 1200 m, La Paz, Bolivia, 12–20 Dec. 1955 (L. Peña), in IRSNB. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange; hardly any black around eyes, except for black pigment behind eye lenses. Chelicerae, labium, endites, sternum light orange. Coxae, legs light orange. Dorsum of abdomen white (Fig. 281); sides and sides of venter with tiny white spots. Eyes small. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.6. Anterior median eyes 1 diameter apart, 2.5 from laterals. Posterior median eyes their diameter apart, 4.5 from laterals. First and second metatarsi and tarsi curved, with more macrosetae on underside than above. Abdomen subspherical (Fig. 281). Total length 8.7 mm. Carapace 3.5 mm long, 2.8 wide. First femur 3.9 mm, patella and tibia 5.0, metatarsus 3.4, tarsus 1.1. Second patella and tibia 4.4 mm, third 2.7, fourth 3.9.

Diagnosis. The hemispherical, entire base of the epigynum in ventral view (Fig. 279) and the small triangular median plate anteriorly fused to the laterals in posterior view (Fig. 280) separate this species from *A. uniformis* (Figs. 272, 273).

Araneus concoloratus (F. P.-Cambridge)
Figures 282–285; Map 3

Aranea concolorata F. P.-Cambridge, 1904: 511, pl. 49, fig. 3, ♀. Female holotype from Veragua. [Cord. Veragua, Serrania de Abasará], Panama, in BMNH, examined. Roewer, 1942: 839.
Araneus concoloratus:—Bonnet, 1955: 462.

Description. Female. Coloration all yellowish white, some black pigment in median eyes, and a white square between epigynum and spinnerets on venter of abdomen (Fig. 285). Eyes small. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes 2.5 diameters apart, 3.5 from laterals. Posterior median eyes slightly less than 2 diameters apart, 5.5 from laterals. Abdomen oval, longer than wide, slightly pointed behind. Total length 8.8 mm. Carapace 4.2 mm long, 3.4 wide. First femur 4.8 mm, patella and tibia 5.7, metatarsus 4.5, tarsus 1.6. Second patella and tibia 4.8 mm, third 3.1, fourth 4.3.

Note. The specimen was probably all green when collected. No other specimen of this species has been found.

Diagnosis. This species differs from the related *A. uniformis* (Figs. 272, 273) and *A. cuiaba* (Figs. 276, 277) by having a shorter scape with parallel sides in the epigynum (Fig. 282) and having the base of the scape overhanging the triangular

posterior median plate in posterior view (Fig. 283).

Araneus sicki new species
Figures 286–289; Map 3

Holotype. Female holotype from Serra dos Órgãos, 1000–1800 m, forest, Est. Rio de Janeiro, Brazil, 19 Apr 1965 (H. Levi), in MZSP, ex MCZ. The species is named after the collector of a paratype, the ornithologist Helmut Sick.

Description. Female paratype. Carapace, chelicerae, labium, endites, and sternum orange. Coxae orange, legs orange with a dark ring on distal half of fourth tibiae. Dorsum of abdomen with white patches (Fig. 288); venter dusky between epigynum and spinnerets (Fig. 289). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes a little more than 1 diameter apart, 1.4 from laterals. Posterior median eyes 0.7 diameter apart, slightly less than 2 from laterals. Abdomen subspherical (Fig. 288). Total length 8.3 mm. Carapace 3.1 mm long, 2.7 wide. First femur 3.7 mm, patella and tibia 4.5, metatarsus 2.7, tarsus 1.0. Second patella and tibia 3.7 mm, third 2.1, fourth 2.9.

Diagnosis. The species differs from all other *Araneus* by having a short wrinkled posterior projection in the epigynum originating from the base of the scape (Figs. 286, 287).

Paratype. BRAZIL *Est. Rio de Janeiro:* Teresópolis, 1600–1800 m, 16 Mar. 1946 (H. Sick, AMNH).

Araneus tijuca new species
Figures 290–294; Map 3

Holotype. Female holotype, male paratype from Barra da Tijuca, Est. Rio de Janeiro, Brazil, sand dunes, shore vegetation, 16 Apr. 1965 (H. Levi), in MZSP, ex MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, and legs yellow. Dorsum of abdomen white with dark cardiac mark and black marks above spinnerets (Fig. 292); sides black; venter with black square, white mark on each side of square and white longitudinal line on each side of white mark (Fig. 293). Posterior median eyes 0.9 diameter of anterior medians, lateral eyes 0.7 diameter. Anterior medians their diameter apart, 1.2 from laterals. Posterior medians 0.5 their diameter apart, a little over 2 from laterals. Abdomen oval. Total length 6.3 mm. Carapace 3.2 mm long, 2.3 wide. First femur 3.4 mm, patella and tibia 3.6, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.2 mm, third 1.9, fourth 2.8.

Male. Color as in female, but no dark marks on dorsum of abdomen. Posterior median eyes 0.7 diameter of anterior medians, lateral eyes 0.6 diameter. Anterior medians 0.8 their diameter apart, 0.8 from laterals. Posterior medians 0.6 their diameter apart, a little less than 2 from laterals. Endite with tooth. Coxa with hook; legs with many dark macrosetae. Second tibia swollen, with four macrosetae in a ventral line, the distal one shortest, proximal longest. Total length 3.9 mm. Carapace 2.2 mm long, 1.7 wide. First femur 2.2 mm, patella and tibia 2.6, metatarsus 1.9, tarsus 0.9. Second patella and tibia 2.6 mm, third 1.4, fourth 2.1.

Note. The photograph of a living female shows the carapace and legs to be dark green, the abdomen green with black areas bordered by white.

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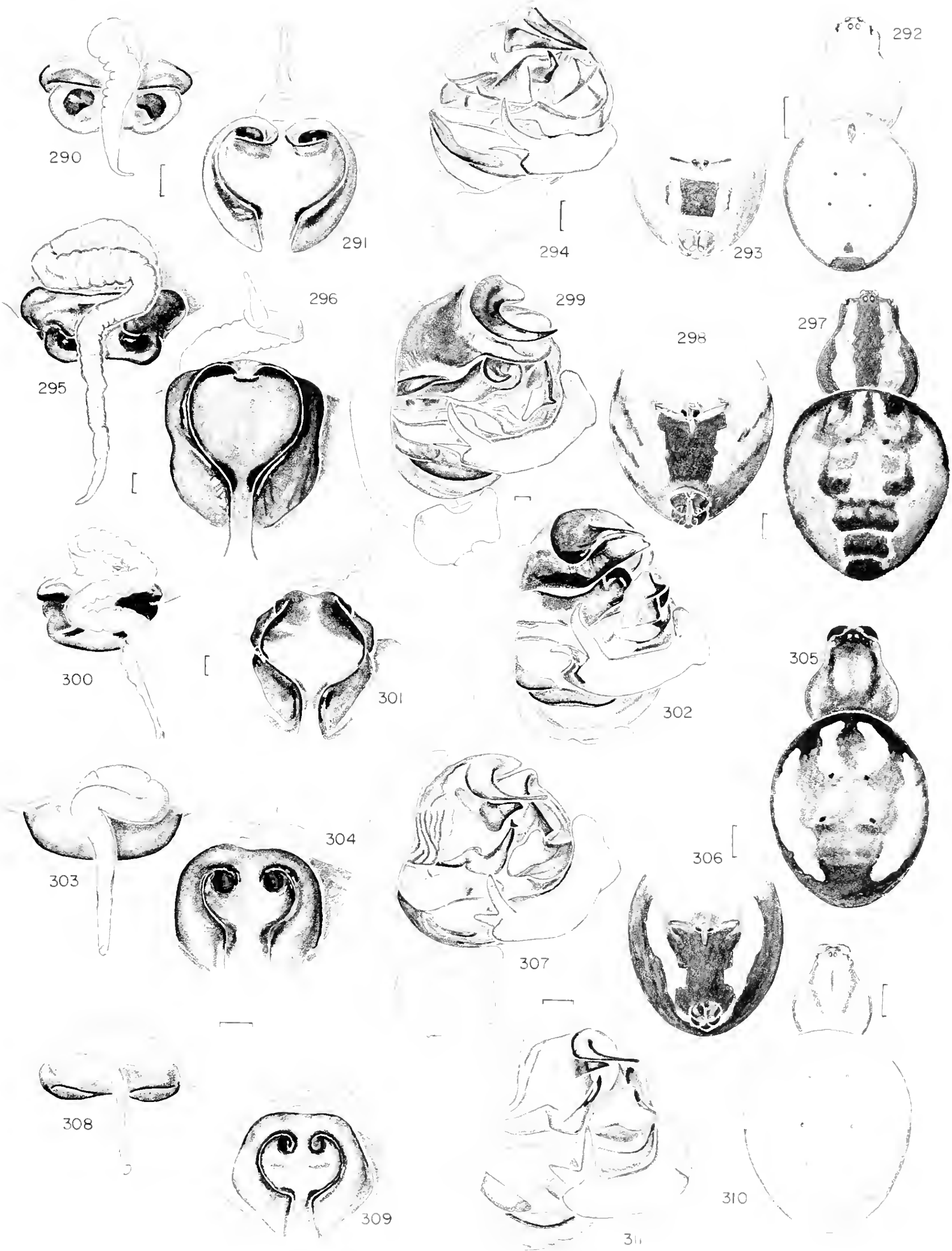
Figures 290–294 *Araneus tijuca* n. sp. 290–293. Female. 290. Epigynum, ventral. 291. Epigynum, posterior. 292. Dorsal. 293. Abdomen, ventral. 294. Male, left palpus.

Figures 295–302 *A. venatrix* (C. L. Koch). 295–298. Female. 295, 300. Epigynum, ventral. 296, 301. Epigynum, posterior. 297. Dorsal. 298. Abdomen, ventral. 299, 302. Male palpus. 295–299 (Panama). 300–302 (São Paulo, Brazil).

Figures 303–311. *A. guttatus* (Keyserling). 303–306, 308–310. Female. 303, 308. Epigynum, ventral. 304, 309. Epigynum, posterior. 305, 310. Dorsal. 306. Abdomen, ventral. 307, 311. Male palpus. 303–307 (Panama). 308–310 (São Paulo, Brazil). 311 (Mato Grosso, Brazil).

Scale lines. 1.0 mm, genitalia 0.1 mm.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Variation. Total length of females 6.3 to 8.0 mm, of males 3.9 to 5.6.

Diagnosis. Females are separated from those of the similar *A. guttatus* (Fig. 300) by the shorter scape of the epigynum (Fig. 290) and by the straight ventral edge of the posterior median plate (Fig. 291). In the male, the median apophysis laterally narrows and the embolus is twisted twice (Fig. 294), unlike in that of *A. guttatus* (Fig. 307).

Natural History. In Rio de Janeiro in the botanical garden at the edge of the forest, a web one meter above ground with the retreat in a folded green leaf, partly shaded.

Distribution. From Espírito Santo to Rio de Janeiro States, Brazil (Map 3).

Paratypes. BRAZIL *Espírito Santo:* M. Moscoso, Vitória, Oct. 1981, ♂ (A. Cerrutti, MNRJ). *Rio de Janeiro:* Itabapoana, ♀ (M. Rosa, MNRJ); Jardim Botânico, Rio de Janeiro, 29–31 Mar. 1983, 2♀ (H. Levi, MCZ); 2 Apr. 1987, 4♀ (H., L. Levi, MCZ).

Araneus venatrix (C. L. Koch)
Plate 2; Figures 295–302; Map 4

Miranda venatrix C. L. Koch, 1839: 56, pl. 373, ♀. Specimens from Brazil, lost.

Epeira analis C. L. Koch, 1845: 75, pl. 891, ♀. Female from Brazil, lost. First synonymized by Keyserling, 1892.

Epeira peruviana Taczanowski, 1878: 150, pl. 1, fig. 5, ♀. Female syntypes from Amable María [Dpto. Junín], Peru, in PAN, examined. NEW SYNONYMY.

Epeira venatrix:—Keyserling, 1892: 201, pl. 9, fig. 149, ♀, ♂.

Araneus venatrix:—Petrunkevitch, 1911: 323.

Araneus sinuoscapus Chamberlin and Ivie, 1936: 49, pl. 14, fig. 123, ♀. Female holotype from Barro Colorado Island, Panama, in AMNH, examined. NEW SYNONYMY.

Aranea peruviana:—Roewer, 1942: 850.

Aranea venatrix:—Roewer, 1942: 855.

Aranea sinuoscapa:—Roewer, 1942: 853.

Araneus venator:—Bonnet, 1955: 627.

Note. Bonnet (1955) writes that in the combination with *Araneus* the specific name has to be declined from *venatrix* to *venator*. Venator means hunter, venatrix means huntress. According to H. D. Cameron (personal communication), venatrix and venator are both nouns not adjectives, and therefore nouns in apposition in the meaning of the *International Code of Zoological Nomenclature* [ICZN 1985, Art. 11 (h, i, 2)]. According to Article 31(b) of the Code, "A species-group name, if it is or ends in a Latin adjective or participle in the nominative singular or is latinized, must agree in gender with the generic name with which it is at any time combined and its termination must be changed according to Latin inflection." H. D. Cameron believes it would be correct if we follow Bonnet. However, while *Araneus venator* is grammatically correct, the ICZN 1985 Art. 31 (b, i) states that as a noun in apposition to the name of its genus, its spelling is not changed if it is combined with a generic name of a different gender. For this reason, I will continue to use the "grammatically incorrect" *Araneus venatrix*.

Description. Female from Panama. Carapace yellow with a median dark band, sides of thorax dark (Fig. 297). Sternum brown. Coxae yellow; legs contrastingly ringed yellow and brown. Dorsum of abdomen with folium consisting of dark bars, shoulders black anteriorly (Fig. 297); sides with coalescent dark spots; venter yellow-brown with black patch between epigynum and spinnerets (Fig. 298). Posterior median eyes 0.8 diameter of anterior medians, lateral eyes 0.7 diameter. Anterior median eyes a little less than their diameter apart, a little less than 2 from laterals. Posterior median eyes 0.6 diameter apart, a little less than 3 from laterals. Abdomen oval (Fig. 297). Total length 12 mm. Carapace 5.0 mm long, 4.3 wide. First femur 5.9 mm, patella and tibia 7.3, metatarsus 5.7, tarsus 1.8. Second patella and tibia 6.5 mm, third 3.9, fourth 6.1.

Male from Panama. Carapace orange, without longitudinal bands. Sternum and legs orange, legs not ringed. Dorsum of abdomen orange-white without pattern, posterior tip black. Sides with black streaks; venter with black square, and white spot on each side of square. Posterior median

eyes 0.7 diameter of anterior medians, lateral eyes 0.6 diameter. Anterior medians a little less than their diameter apart, their diameter from laterals. Posterior median eyes 0.7 diameter apart, a little more than 2 from laterals. Endite with tooth. First coxa with hook. Second tibia swollen, with macrosetae. Total length 8.6 mm. Carapace 4.7 mm long, 3.8 wide. First femur 5.0 mm, patella and tibia 6.5, metatarsus 4.5, tarsus 1.3. Second patella and tibia 6.2 mm, third 3.4, fourth 5.2.

Note. The photograph of a living female from Brazil (Plate 2) shows the abdomen to have white and black marks with red and brown spots. A male from Panama has the first right leg regenerated.

Variation. Total length of females 8.0 to 16.7 mm, of males 6.1 to 8.1. Figures 295–299 were made from a specimen from Panama, 300 and 301 from São Paulo, 302 from Rio Grande do Sul.

Diagnosis. Living specimens have an oval abdomen with distinct transverse bars on the posterior. The female has a coiled scape as does *A. guttatus* (Fig. 303), but the anterior edge of the median plate differs in posterior view (Figs. 296, 301). The male has the median apophysis laterally expanded, as does *A. guttatus* (Fig. 307), but differs by the coiled tip of the embolus seen below the subterminal apophysis (Figs. 299, 302).

Natural History. The large web is often found near water. Like other large *Araneus* species, the female sits in a retreat.

Distribution. From Panama, Trinidad to Rio Grande do Sul, Brazil, and Paraguay (Map 4).

Records. PANAMA *Panamá:* Barro Colorado Island (MCZ); Summit (MCZ); Madden Dam (MCZ); Forest Reserve (MCZ); Cerro Galero, Arraiján (MCZ). TRINIDAD Port of Spain (MCZ); Navy Base (AMNH); Sangre Grande (AMNH); Maracas Valley (AMNH); Arima Valley (AMNH); Ft. George Hill (AMNH). VENEZUELA *Amazonas:* Cerro de la Neblina, base camp, 140 m (USNM). GUYANA *Bartica Distr.:* Kartabo (AMNH). SURINAM *Brokopondo:* Brownsberg (MCZ). *Saramacca:* Voltzberg-Raleighvallen Reserve (MCZ). FRENCH GUIANA nr. Cayenne (MCZ). COLOMBIA *Meta:* Puerto Lleras [33°16′N, 73°23′W] (MCZ); 15 km SW Puerto López, 200 m (MCZ). *Caquetá:* Río Orteguaza (AMNH). ECUADOR *Napo:* Res. Faunistica Cuyobeno (MCZ, MECN). PERU *Loreto:* Iquitos (MCZ). *Amazonas:* Alto Río Comaina, 850–1150 m (MHNSM). *San Martín:* 20 km NE Moyobamba (AMNH). *?Ucayali:* Concha Huaya, Río Ucayali [?] (BMNH). *Pasco:* Huancabamba, 345 m (BMNH). BRAZIL *Pará:* Óbidos (MZSP). *Roraima:* Rio Branco, Serra Grande (NHRM). *Amazonas:* Maués (INPA); Rio Negro, Umarituba (NHRM); Rio Autás, Santa Amélia [Autás Mirim] (NHRM). *Rondônia:* Abunã (MCZ). *Bahia:* Uruçuca (MCN). *Espírito Santo:* Santa Teresa (AMNH); Morro Moscoso, Vitória (MCN, MNKJ). *Rio de Janeiro:* Nova Friburgo (MNRJ); Rio de Janeiro (MNRJ, MCZ, AMNH); Teresópolis (AMNH); Parque Nac. Tijuca (MCZ). *São Paulo:* Borneri (MZSP); Bosque Sander (MZSP); São Roque (MZSP); Barueri (MZSP); São Paulo (MZSP, MCZ, AMNH); Diadema (MZSP); São Bernardo, Estr. do Mar (MZSP, MCZ); Nova Europa (MZSP); Cocaia (MZSP); Boracéia (MZSP); Salesópolis (MZSP); Itu (AMNH). *Paraná:* Terra Bôa, Almirante Tamandaré (MCN). *Santa Catarina:* Pinhal (AMNH). *Rio Grande do Sul:* Porto Alegre (MCN); Aguas Belas Viãmao (MCN); Parque Est. do Turvo (MCN); Caxias do Sul (MCN); Pelotas (MCZ). PARAGUAY *Concepción:* Apa (AMNH). *Paraguarí:* Ybycuí Natl. Pk. (MCZ, IBNP). BOLIVIA *Beni:* Chacobo Indian Village, Río Benicito (AMNH); Cavinas (USNM). ARGENTINA *Misiones:* Parque Nac. Iguazu (MEG, CAS).

Araneus guttatus (Keyserling)
Plate 2; Figures 303–315; Map 4

Epeira guttata Keyserling, 1865: 823, pl. 18, figs. 17, 18, ♀. Female holotype without epigynum from New Granada [Spanish colony of Panama, Colombia], in BMNH, examined.

Epeira similis Taczanowski, 1872: 130. Female lectotype here designated from Cayenne, French Guiana in PAN, examined. Name preoccupied by Blackwall, 1844. NEW SYNONYMY.

Aranea glabrata F. P.-Cambridge, 1904: 512, pl. 49, fig. 6, ♀. Female holotype from Bugaba, Panama, in BMNH, lost. Roewer, 1942: 843. NEW SYNONYMY.

Aranea guttata:—Roewer, 1942: 844.

Aranea similella Roewer, 1942: 852. New name for *E. similis* Taczanowski. NEW SYNONYMY.

Neosconella bipunctata Mello-Leitão, 1948: 170, fig. 12, ♀. Female holotype from Kutuabatu Creek [?Kutuau Creek], British Guiana, in BMNH, examined. NEW SYNONYMY.

Araneus guttatus:—Bonnet, 1955: 513.

Araneus leitaoi Brignoli, 1983: 263. New name for *N. bipunctata*, which is preoccupied in the combination *Araneus bipunctatus* Thorell, 1898. NEW SYNONYMY.

Note. The holotype of *A. guttatus* has lost its epigynum; however, this structure was illustrated by Keyserling. Keyserling's illustration and the markings on the holotype leave no doubt about the identity of this common, widespread species.

Description. Female from Panama. Carapace marbled dark brown on yellow, sternum dark brown. Coxae yellow; legs yellow ringed brown to black, distal half black. Dorsum of abdomen with folium (Fig. 305); venter black with two white spots (Fig. 306). Carapace glabrous. Secondary eyes 0.7 diameter of anterior median eyes. Anterior median eyes slightly more than their diameter apart, 1.5 from laterals. Posterior median eyes a little less than their diameter apart, 2.5 from laterals. Abdomen oval, with few hairs. Total length 8.7 mm. Carapace 3.8 mm long, 2.9 wide. First femur 3.2 mm, patella and tibia 4.0, metatarsus 2.9, tarsus 1.2. Second patella and tibia 3.7 mm, third 2.3, fourth 3.2.

Male from Panama. Color as in female. Thoracic depression present but indistinct. Secondary eyes 0.7 diameter of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 0.8 from laterals. Posterior median eyes 0.7 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first. Abdomen oval. Total length 4.8 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.9 mm, patella and tibia 3.7, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.1 mm, third 1.7, fourth 2.5.

Variation. A photograph of a female from Panama (Plate 2) shows the abdomen white with a yellowish green cast and black marks; that of a Colombian specimen is green. Kochalka reports (personal communication) specimens from Paraguay with a brilliant green and black abdomen; the carapace may be yellow-green, the legs orange.

Specimens in alcohol from Brazil are pale dorsally on the abdomen (Fig. 310). Also the ventral white spots are more anterior on the middle of the sides of the black patch. The genitalia (Figs. 308, 309 from São Paulo, 311 from Mato Grosso) are similar to those of specimens from Panama (Figs. 303, 304, 307).

Figures 312–315 were made from a specimen from Huachipa, Peru (CAS), first thought distinct. Another came from Alto Solimões, Brazil (MCN). The type of *Epeira similis* from Cayenne has a median plate of the same shape. A male, if collected with such females, may have characters that tell whether the specimens belong to a distinct species. Total length of females 5.2 to 13.5 mm, of males 3.8 to 6.5. The largest individuals came from Mato Grosso, Brazil.

Diagnosis. Females differ from *A. venatrix* (Figs. 295, 296) and *A. tijuca* (Figs. 290, 291) by the ventral border of the median plate of the epigynum, which in *A. guttatus* curls toward the median, forming two dark circles (Figs. 304, 309, 313); males differ by the cone-shaped embolus (Figs. 307, 311).

Natural History. In Panama specimens have been collected from gardens and a forest, females in a retreat in a curled leaf. In Paraguay, where it is found in an undisturbed low forest, the female builds only a flimsy retreat in vegetation (Kochalka, personal communication). Most collecting localities are at low elevations.

Distribution. From Costa Rica to Río Negro, Argentina (Map 4).

Records. COSTA RICA *San José:* San Isidro del General, 700–800 m (AMNH). PANAMA *Veraguas:* Santiago (MIUP); El Salto, San Francisco de la Montaña (MIUP). *Colón:* Ft. Davis (MCZ). *Panamá:* very common (MCZ, AMNH, MIUP). *Darién:* Villa Darién [?] (MIUP). VENEZUELA *Distríto Federal:* Caracas (USNM). GUYANA Kartabo (AMNH). COLOMBIA *Magdalena:* Ciénaga (MCZ); San Pedro, 1200 m (JAK). *Cesar:* Finca San José, 8 km SE Socorpa Mission, Sierra de Perijá, 1450–1500 m (AMNH). *Córdoba:* Ayapel nr. Ciénaga "La Guajade" (MHNMC). *Antioquia:* Turbo, oil palm (MCZ); Mutatá (MCZ). *Santander:* Río Suárez, 800–1000 m (AMNH). *Meta:* ca. 15 km SW Puerto López (MCZ). *Valle:* 20 km E, 28 km E Buenaventura, both (MCZ); Sevilla (AMNH). *Caquetá:* Río Orteguaza (AMNH). *Putumayo:* Buena Vista (MCZ). *Amazonas:* Araracuara, 270 m (CV). ECUADOR *Napo:* Coca (MCZ); Cuyabeno, Tarapoa (MCZ, MECN). PERU *Loreto:* Iquitos (MCZ). *Amazonas:* Alto Río Comaina, 850–1150 m (MHNSM). *Ucayali:* Pucallpa (MHNSM, AMNH); Ucayali Parque Nac. von Humboldt (MHNSM). *Huánuco:* La Molina, SW Pto. Inca, 270 m (MHNSM). *Pasco:* Huancabamba (MHNSM). *Madre de Dios:* Tambopata Res., 290 m (MCZ, MNHSM); Atalaya (MHNSM). BRAZIL *Amazonas:* Manaus, Reserva Duche (MEG). *Rondônia:* Abunã (MCZ). *Goiás:* San Francisco Jara (MZSP). *Mato Grosso:* Lagoa Ipari, Parque Nac. de Xingu (MZSP); Barra do Tapirapé (AMNH); Confl. Araguaia e Tapirapé (MZSP). *Minas Gerais:* Lagõa Santa (MZSP). *Rio de Janeiro:* Rio de Janeiro (ZMK). *São Paulo:* Diadema (MZSP); Jundiaí (MCZ, MNRJ, MZSP); Cocaia (MZSP); Barueri (MZSP). *Paraná:* Rolândia (MZSP). *Rio Grande do Sul:* Santa Rosa (AMNH); Santa Maria (MCN); Garruchos, São Borja (MCN). PARAGUAY *Chaco:* Transchaco km 189, km 20 (IRSNB); Parque Nac. Defensores del Chaco: Madrejón (IBNP). *Concepción:* Apa (AMNH); Fonciere (MCZ). *Alto Paraná:* Itaho Reserve (IRSNB); km 12 de Stroessner (IBNP); Taquararapa (AMNH). *Central:* San Lorenzo (IBNP). *Paraguarí:* Sapucay (MACN); Ybycuí (IBNP); Ybycuí Natl. Pk. (MCZ). *Itapúa:* Antidia Matiauda, 20 km NE Puerto Capitán Mesa (MCZ). *Ñeembucú:* Monte Rita (ZMK). ARGENTINA *Misiones:* Parque Nac. Iguazu (MEG); Candelaria (MACN); R. Rico (MACN); Montecarlo (AMNH). *Río Negro:* El Bolsón (AMNH).

Araneus abeicus new species
Figures 316–320; Map 3

Holotype. Female holotype, two female and one male paratypes from Boracéia, Est. São Paulo, Brazil, 22–23 Feb. 1961 (P. Biasi), in MZSP no. 1228. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace light orange, head brown with V-shaped white pigment mark. Chelicerae orange. Labium, endites brown. Sternum orange with a median white pigment mark, border darker. Coxae orange; legs orange with brown rings. Dorsum of abdomen white with black marks (Fig. 318); venter with two white bands, black between (Fig. 319). Posterior median eyes same diameter as anterior medians, anterior laterals 1 diameter, posterior laterals 0.7. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes their diameter apart, 1.8 from laterals. Abdomen slightly longer than wide with a pair of humps (Fig. 318). Total length 4.2 mm. Carapace 2.0 mm long, 1.5 wide. First femur 1.9 mm, patella and tibia 2.4, metatarsus 1.5, tarsus 0.8. Second patella and tibia 1.9 mm, third 1.2, fourth 1.9.

Male. Color as in female. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.5 diameter, posterior laterals 0.6. Anterior median eyes 0.8 diameter apart, 0.7 from laterals. Posterior median eyes their diameter apart, 1.5 from laterals. Endite with tooth. First coxa with small hook. Second tibia thicker than first,

with some macrosetae. Abdomen oval, humps less distinct than those of female. Total length 3.6 mm. Carapace 1.7 mm long, 1.5 wide. First femur 1.7 mm, patella and tibia 2.4, metatarsus 1.5, tarsus 0.7. Second patella and tibia 1.8 mm, third 1.2, fourth 1.6.

Diagnosis. Araneus abeicus females differ from those of *A. iguacu* (Figs. 321, 322) and *A. lenkoi* (Figs. 326, 327), in that the epigynum has two bulges on the posterior margin, one on each side of the scape (Fig. 316). Lateral and median plates are fused in posterior view (Fig. 317). The median apophysis is small and has three teeth (Fig. 320), unlike that of *A. iguacu* (Fig. 325), and the embolus appears to be an enormous structure perhaps derived from the lamella or the base of the embolus, a wrapper enclosing a filament (Fig. 320).

Paratypes. One ♀ from type locality, 28 Feb. 1967 (P. Biasi, MZSP 6117).

Araneus iguacu new species
Plate 2; Figures 321–325; Map 3

Holotype. Female holotype, male and two immature paratypes from near Saltos do Iguaçu, Est. Paraná, Brazil, 24 Mar. 1985 (H., L. Levi), in MZSP. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace light orange with paired dusky marks and a white pigment patch (Fig. 323). Chelicerae, labium, endites orange. Sternum light orange, sides dusky, with white pigment spot. Coxae light orange; legs light orange with indistinct dusky rings. Dorsum of abdomen with dusky pattern (Fig. 323); venter with four white marks and white spots (Fig. 324). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.8. Anterior median eyes slightly more than their diameter apart, the same from laterals. Posterior median eyes 0.6 diameter apart, slightly less than 2 from laterals. Abdomen subspherical with a pair of dorsal humps (Fig. 323). Total length 4.5 mm. Carapace 2.0 mm long, 1.6 wide. First femur 1.8 mm, patella and tibia 2.3, metatarsus 1.6, tarsus 0.6. Second patella and tibia 1.9 mm, third 1.2, fourth 1.8.

Male paratype. Color as in female except abdomen lacks dusky marks. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.4 diameter, posterior laterals 0.5. Anterior median eyes 0.7 diameter apart, 0.7 from laterals. Posterior median eyes 0.7 diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia thicker than first with several macrosetae. Abdomen longer than wide with two humps. Total length 2.9 mm. Carapace 1.4 mm long, 1.3 wide. First femur 1.7 mm, patella and tibia 2.1, metatarsus 1.4, tarsus 0.5. Second patella and tibia 1.6 mm, third 0.9, fourth 1.3.

Note. A photograph (Plate 2) shows the live female to be bright green with black and white marks.

Diagnosis. All females of this species examined had a wide scar of a scape torn

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Figures 312–315. *Araneus guttatus* (Keyserling), female (Huanuco, Peru). 312. Epigynum, ventral. 313. Epigynum, posterior. 314. Dorsal. 315. Abdomen, ventral.

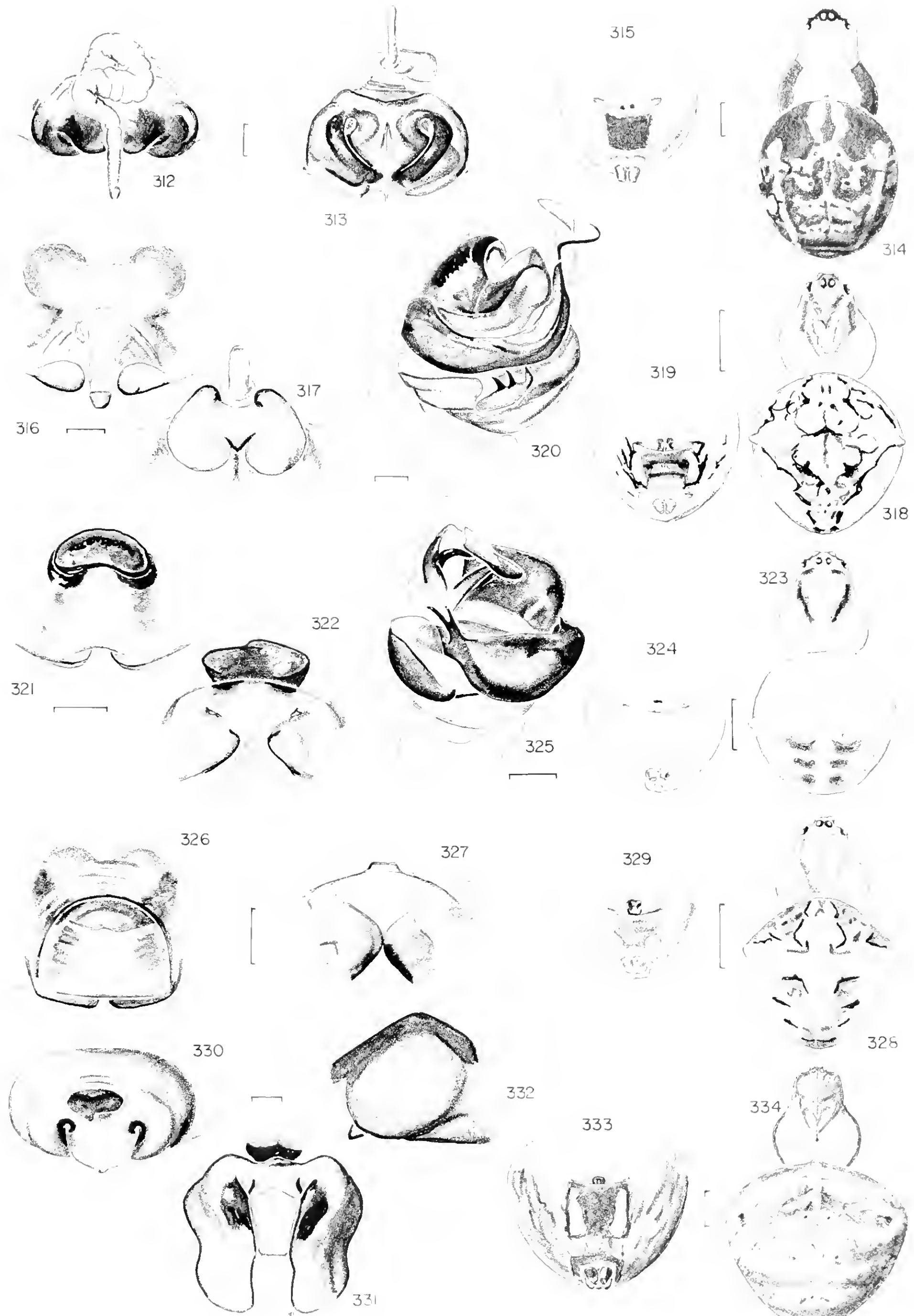
Figures 316–320. *A. abeicus* n. sp. 316–319. Female. 316. Epigynum, ventral. 317. Epigynum, posterior. 318. Dorsal. 319. Abdomen, ventral. 320. Male, left palpus.

Figures 321–325. *A. iguacu* n. sp. 321–324. Female. 321. Epigynum, ventral. 322. Epigynum, posterior. 323. Dorsal. 324. Abdomen, ventral. 325. Male palpus.

Figures 326–329. *A. lenkoi* n. sp., female. 326. Epigynum, ventral. 327. Epigynum, posterior. 328. Dorsal. 329. Abdomen, ventral.

Figures 330–334. *A. chingaza* n. sp., female. 330. Epigynum, ventral. 331. Epigynum, posterior. 332. Epigynum, lateral. 333. Dorsal. 334. Abdomen, ventral.

Scale lines: 1.0 mm, genitalia 0.1 mm.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off (Fig. 321). The epigynum differs from that of *A. lenkoi* (Figs. 326, 327) by having a central depression posterior to the scar of a wide scape (Fig. 321). The male has a large semicircular median apophysis with two fine hooks mesally near its base (Fig. 325).

Natural History. The web, about 12 cm in horizontal diameter (Plate 2), is made on overhanging cliffs with the retreat above in a crevice. The bottom of the orb is farther from the cliff than the top. It may lack a signal line. Some other webs have an open sector with a signal line, similar to a *Zygiella* web.

Paratypes. BRAZIL *Rio de Janeiro:* Parque Nacional Tijuca, Alto de Boa Vista, 1 Apr. 1987, 6♀ (H., L. Levi, MCZ, MNRJ). *Paraná:* nr. Saltos do Iguaçu, 22 Mar. 1985, ♀ (H., L. Levi, MCZ); 23 Mar. 1985, ♀, ♂ (H., L. Levi, MCN). ARGENTINA *Misiones:* Cataratas de Iguazú, Sept. 1963, ♀ (M. E. Galiano, MEG).

Araneus lenkoi new species
Figures 326–329; Map 3

Holotype. Female holotype from Boracéia, Est. São Paulo, Brazil, 1 Feb. 1961 (K. Lenko), in MZSP no. E 3373. The species is named after the collector.

Description. Female. Carapace orange with dusky mark on head narrowing posteriorly. Chelicerae, labium, endites, sternum orange. Coxae orange; legs light orange indistinctly ringed darker. Dorsum of abdomen with white and black pattern (Fig. 328); venter dusky with a pair of white spots (Fig. 329). Posterior median eyes 1.2 diameters of anterior medians, laterals 1 diameter. Anterior median eyes 1 diameter apart, slightly more than 1 from laterals. Posterior median eyes slightly less than their diameter apart, 1.8 from laterals. Abdomen longer than wide with two humps (Fig. 328). Total length 3.5 mm. Carapace 1.7 mm long, 1.4 wide. First femur 1.7 mm, patella and tibia 2.1, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.7 mm, third 1.0, fourth 1.6.

Note. The right first leg of the holotype is regenerated and shorter than the left one. The epigynum has a thin, transparent scape with parallel sides within a semicircular depression; the scape does not extend beyond the genital groove. It broke and was lost when cleaning the epigynum with a brush before illustrating.

Diagnosis. This species is similar to *A. iguacu* (Figs. 321, 322) but differs by having a narrow scape with parallel sides and by having paired dark marks anterior to the semicircular depression (Fig. 326).

Araneus chingaza new species
Figures 330–334; Map 3

Holotype. Female from Paramo de Chingaza, 3000 m, Dpto. Cundinamarca, Colombia [4°31′N, 73°45′W], between rocks, 19 Oct. 1986 (C. Valderrama A.) in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellowish, head with dusky marks and white and black setae, rim of thorax black. Chelicerae proximally light, dark brown distally. Labium, endites dark brown. Sternum dark brown, lighter in middle. Coxae yellowish with dark patches. Legs with irregular incomplete dark rings on yellowish. Dorsum of abdomen with indistinct transverse brown bands, small brown spots and some white pigment (Fig. 333); venter black with a white line on each side, streaks on the sides (Fig. 334). Secondary eyes 0.8 diameter of anterior medians. Anterior median eyes 1 diameter apart, 1.6 from laterals. Posterior median eyes 1.2 diameters apart, 2.5 from laterals. Abdomen as wide as long, with humps. Total length 8.2 mm. Carapace 3.4 mm long, 2.6 wide. First femur 3.2 mm, patella and tibia 4.0, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.7 mm, third 2.2, fourth 3.2.

Diagnosis. The male of this species is unknown; the female has the scape of the epigynum torn, making it difficult to relate this species to others. However, the small pentagonal median plate in posterior view (Fig. 331) and the openings as seen in ventral view (Fig. 330) distinguish this species from others.

Araneus selva new species
Figures 335–338; Map 5

Holotype. Female from Finca La Selva, near Puerto Viejo, Heredia Prov., Costa Rica, 50 m, Jan. 1978 (W. Eberhard no. 1262), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace light yellowish, no dark pigment around eyes. Sternum, legs, light yellowish. Dorsum of abdomen white; venter white, no pigment around epigynum or around spinnerets (Fig. 337). Eyes small. Posterior median eyes same diameter as anterior medians, lateral eyes 0.9 diameter. Anterior medians their diameter apart, 1.2 from laterals. Posterior medians 0.5 diameter apart, 2 from laterals. Abdomen wider than long (Fig. 337). Total length 3.3 mm. Carapace 1.4 mm long, 1.2 wide. First femur 1.6 mm, patella and tibia 1.8, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.5 mm, third 1.0, fourth 1.3.

Male from Finca La Selva. Coloration as in female, but legs with dusky rings. Carapace has a dusky M-shaped mark, with its lateral arms along edge of carapace. Dorsum of abdomen white with dusky spots all around; venter with white pigment spots. Posterior median eyes same diameter as anterior medians, lateral eyes 0.7 diameter. Anterior medians 0.8 their diameter apart, 0.5 from laterals. Posterior medians a little less than their diameter apart, a little less than 2 from laterals. Palpus with 2 long patellar setae. Endite with tooth. Axis of coxal hook parallel to axis of first coxa. Legs with long black setae. Second tibia with long macrosetae. Total length 2.1 mm. Carapace 1.1 mm long, 1.0 wide. First femur 1.2 mm, patella and tibia 1.4, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.0 mm, third 0.7, fourth 0.9.

Variation. Total length of females 2.7 to 3.5 mm, of males 2.1 to 2.7. Some females from the type locality have a thinner, longer scape than the holotype illustrated. The lateral plates of the epigynum may be a variable distance apart.

Diagnosis. The shiny, large oval lateral plates in posterior view (Fig. 336) and the oval base of the epigynum (Fig. 335) separate females from other small species. The male palpus has a large median apophysis diagonal in position with a spine on each end and a distinctive large conductor (Fig. 338). The median apophysis resembles that of the North American *A. pratensis* (Levi, 1973, fig. 30), but the abdomen of *A. pratensis* is longer than wide.

Natural History. Females have been collected from beneath a tree at the edge of a jungle in Guatemala, and from vegetation in a stream bed at the Osa Peninsula in Costa Rica. Some specimens were collected at night. A female from Turrialba has 13 nonagglutinated eggs in her egg-sac.

Paratypes. GUATEMALA Tikal, 7 July 1965, ♂ (W. Sedgwick, MCZ). COSTA RICA *Heredia:* Finca La Selva, Dec. 1982, ♂ (W. Eberhard, MCZ); 9 Oct. 1981, ♀ (C. Griswold AR-29, MCZ); Jan. 1978, ♀ (W. Eberhard 1299, MCZ). *Cartago:* Turrialba, 11 Mar. 1967, ♀ (W. Peck, CAS); 14 Mar. 1967, ♂ (W. Peck, CAS). *Puntarenas:* Rincon, Osa, nr. R. Agua Buena, 18 Feb. 1973, ♀ (W. Eberhard, MCZ).

Araneus sextus (Chamberlin)
Figures 339–342; Map 5

Aranea sexta Chamberlin, 1916: 255, pl. 19, fig. 7, imm. Immature female holotype from Panama, in MCZ, examined. Roewer, 1942: 852.
Araneus sextus:—Bonnet, 1955: 598.

Description. Female. Carapace streaky orange. Sternum and legs orange. Dorsum of abdomen white and orange, transversely banded (Fig. 341). Venter orange with white pigment. Eyes subequal. Anterior medians a little less than 2 diameters apart, 2 from laterals. Posterior medians their diameter apart, a little more than 2 from laterals. Three very long anterior teeth on chelicerae. Prolateral and dorsal sides of tibiae, metatarsi, and tarsi with field of long and short setae. Abdomen wider than long, with lateral pointed humps (Fig. 341). Total length 6.0 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.8 mm, patella

and tibia 3.8, metatarsus 2.2, tarsus 0.8. Second patella and tibia 2.8 mm, third 1.6, fourth 2.2.

Male. Coloration as in female, but legs indistinctly ringed and abdomen with less dark pigment. Eyes subequal. Anterior medians 1.5 diameters apart, 1.4 from laterals. Posterior medians a little less than their diameter apart, 1.5 from laterals. Endite without tooth. No hook on first coxa. Second tibia not modified. Abdomen subspherical, with tubercle on each shoulder. Total length 1.8 mm. Carapace 0.9 mm long, 0.8 wide. First femur 1.0 mm, patella and tibia 1.1, metatarsus 0.7, tarsus 0.4. Second patella and tibia 0.9 mm, third 0.5, fourth 0.7.

Note. Photograph showed a living female from Manaus to be orange-brown and white (H. Höfer, photograph).

Variation. Total length of females 6.0 to 8.3 mm, of the much smaller males 1.7 to 2.7.

Diagnosis. The shape of the abdomen, unlike other Neotropical *Araneus* species, resembles that of *Epeiroides bahiensis* (Keyserling) (Levi, 1989) but the epigynum, with a small stump of a scape (Fig. 339), differs. The median apophysis of the male palpus has a spine directed "down" (facing the cymbium), and is frayed at the lateral end (Fig. 342).

Natural History. This species has been found in low elevation forests, one record from 1700 m elevation.

Distribution. Guatemala to Manaus, Brazil (Map 5). both Roewer (1942) and Bonnet (1955) erroneously list the species as occurring in Peru. No such record exists; although published in a paper on Peruvian spiders, the holotype specimen came from Panama.

Records. GUATEMALA *Escuintla:* Tiquisate, June 1947, ♀ (C., P. Vaurie, AMNH). PANAMA *Panamá:* El Valle, July 1936, ♀; Arraiján, 6 July 1950, ♀; Corozal, 4 Jan. 1958, ♂; Summit, Aug. 1950, ♂; nr. Cocoli, 13 Jan. 1958, ♂; Diablo Heights, 19 Dec. 1957, ♂ (all A. M. Chickering, MCZ). COLOMBIA *Antioquia:* La Estrella, 1700–1880 m, June–Aug. 1974, ♂ (P. A. Schneble, MCZ). BRAZIL *Amazonas:* Manaus, Paspalum, 26 Feb. 1987, ♀ (H. Höfer, INPA).

Araneus microsoma (Banks)
Figures 343–346; Map 5

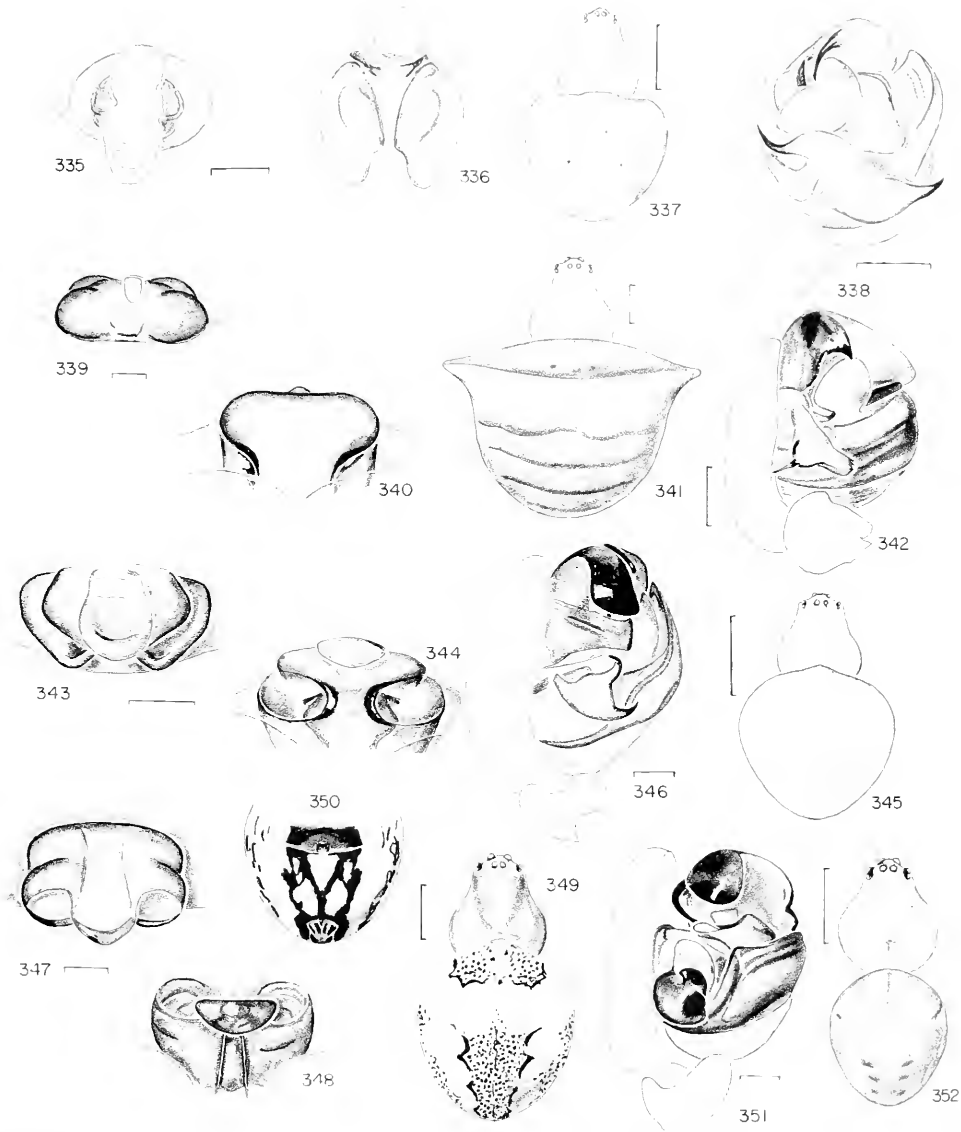
Epeira microsoma Banks, 1909: 211, pl. 6, figs. 39, 45, ♀, ♂. Male holotype and female paratype from bushes, La Palma [Prov. Cartago, 15 km NE of San José], Costa Rica, in MCZ, examined.
Aranea microsoma:—Roewer, 1942: 847.
Araneus microsoma:—Bonnet, 1955: 544.

Description. Female. All orange, sternum slightly dusky, abdomen lighter than carapace. Eyes small. Posterior median eyes 2.2 and 1.5 diameters of anterior medians (left and right eyes are different sizes), laterals 1 diameter. Anterior median eyes 2 diameters apart, 2.5 from laterals. Posterior median eyes separated by 0.7 diameter of the larger eye, slightly less than 2 diameters from laterals. Abdomen as wide as long, with indistinct humps (Fig. 345). Total length 2.8 mm. Carapace 1.1 mm long, 0.8 wide. First femur 1.3 mm, patella and tibia 1.5, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.8, fourth 1.1.

Male. Coloration as in female. Venter of abdomen slightly dusky. Eyes small, subequal. Anterior median eyes slightly less than their diameter apart, 1.5 from laterals. Posterior median eyes their diameter apart, 1.8 from laterals. Endite with indistinct tooth. First coxa without hook. Second tibia thinner than first, with a few macrosetae. Abdomen oval, longer than wide. Total length 2.1 mm. Carapace 1.1 mm long, 1.0 wide. First femur 1.4 mm, patella and tibia 1.6, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.7, fourth 1.1.

Banks described the male's abdomen as yellow-brown with an indistinct dark brown median area containing a pair of yellow spots.

Diagnosis. In posterior view, the epigynum has two transverse oval depressions (Fig. 344). The median apophysis of the



Figures 335–338. *Araneus selva* n. sp. 335–337. Female. 335. Epigynum, ventral. 336. Epigynum, posterior. 337. Dorsal. 338. Male, left palpus.

Figures 339–342. *A. sextus* (Chamberlin). 339–341. Female. 339. Epigynum, ventral. 340. Epigynum, posterior. 341. Dorsal. 342. Male, left palpus.

Figures 343–346. *A. microsoma* (Banks). 343–345. Female. 343. Epigynum, ventral. 344. Epigynum, posterior. 345. Dorsal. 346. Male palpus.

Figures 347–350. *A. lintatus* n. sp., female. 347. Epigynum, ventral. 348. Epigynum, posterior. 349. Dorsal. 350. Abdomen, ventral.

Figures 351, 352. *A. chiapas* n. sp., male. 351. Palpus. 352. Dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

male has two spines, both directed laterally (Fig. 346).

Araneus lintatus new species
Figures 347–350; Map 5

Holotype. Female holotype from mountain near Asia [12°07'S, 76°30'W], Dpto. Lima, Peru (W. Weyrauch), in AMNH. The specific name is an arbitrary combination of letters.

Description. Female. Carapace dusky orange, sides of head darker. Chelicerae dusky orange. Labium, endites black. Sternum black with median longitudinal light streak. Coxae orange; legs dusky orange with black spots and some fine black rings. Dorsum of abdomen white with a spotted area anteriorly and a spotted folium posteriorly (Fig. 349). Venter black with a triangular white patch posterior to epigynum, and pairs of white patches; sides light and streaked (Fig. 350). Posterior median and anterior lateral eyes same diameter as anterior medians, posterior laterals 0.8 diameter. Anterior median eyes 1.3 diameters apart, 1.3 from laterals. Posterior median eyes 0.5 diameter apart, slightly more than 2 from laterals. Abdomen oval, longer than wide with a slight anterior median hump (Fig. 349). Total length 4.7 mm. Carapace 2.0 mm long, 1.6 wide. First femur 2.1 mm, patella and tibia 2.5, metatarsus 1.8, tarsus 0.9. Second patella and tibia 2.3 mm, third 1.3, fourth 2.0.

Diagnosis. The female is distinguished by the scape, the sides of which appear fused to the base of the epigynum (Fig. 347).

Araneus chiapas new species
Figures 351, 352; Map 5

Holotype. Male from 5 km W of San Cristóbal de las Casas on Hwy. 190, Chiapas, Mexico [92°41'W, 16°44'N], 2100 m, oak-pine woodland (W. Maddison, R. S. Anderson, 83-126), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace and legs orange, sternum dusky orange. Dorsum of abdomen with a chevron consisting of two white lines anteriorly, and a transverse white line in center; dusky paired patches posteriorly. Venter pale dusky orange, without marks. Posterior median eyes same diameter as anterior medians, lateral eyes 0.8 diameter. Anterior median eyes 0.8 their diameter apart, their diameter from laterals. Posterior median eyes 0.7 diameter apart, 2 from laterals. Endite with tooth. First coxa without hook. First tibia thicker than second, with macrosetae. Abdomen spherical with two indistinct humps. Total length 3.1 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.4 mm, patella and tibia 2.1, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.7 mm, third 0.9, fourth 1.3.

Diagnosis. The two wide, sclerotized lobes of the median apophysis separate this male from others (Fig. 351).

Araneus bryantae Brignoli
Figures 353–356; Map 5

Neosconella parva Bryant, 1945: 381, figs. 19, 24, ♀. Female holotype from foothills and Cordillera Central, S of Santiago, Dominican Republic, in MCZ, examined.

Araneus bryantae Brignoli, 1983: 262. New name for *Neosconella parva* since preoccupied by *Araneus parva* Karsch, 1878.

Description. Female. Carapace orange, dusky on sides. Chelicerae orange. Labium, endites dusky. Sternum dark dusky. Coxae, legs orange. Dorsum of abdomen with large white patch and paired dusky patches on each side of white patch (Fig. 355); venter dusky with a white longitudinal band on each side (Fig. 356). Posterior median and lateral eyes same diameter as anterior medians. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes their diameter apart, 2.7 from laterals. Abdomen oval, longer than wide (Fig. 355). Total length 4.0 mm. Carapace 1.5 mm long, 2.7 wide. First femur 1.7 mm, patella and tibia 2.1, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.9 mm, third 1.1, fourth 1.7.

Variation. The holotype has the abdomen about as wide as long; the abdomen of the paratype is longer than wide.

Diagnosis. This species is distinguished from *A. elizabethae* (Figs. 357, 358) and *A. hotteiensis* (Figs. 361, 362) by the wide scape, which narrows posteriorly (Fig. 353).

Distribution. Hispaniola (Map 5).

Record. GREATER ANTILLES *Dominican Republic:* Loma Rucilla Mts., Cord. Central, 1600–2600 m, June 1938, ♀ (P. J. Darlington, MCZ).

Araneus elizabethae new name
Figures 357–360; Map 5

Meta blanda Bryant, 1945: 386, fig. 22, ♀. Female holotype from Kenscoff, Ouest, Haiti, 1400 m, in MCZ, examined. The species is named after E. Bryant.

Meta bryantae Brignoli, 1983. New name for *blanda*, preoccupied by *Meta blanda* L. Koch, 1878, and *Araneus blandus* (Blackwall, 1865), but also preoccupied in the combination *Araneus bryantae* by Brignoli, 1983.

Description. Female. Carapace yellow with a dusky patch, edge of thorax dusky. Sternum black. Coxae and legs yellow. Dorsum of abdomen with wide white longitudinal and transverse bands forming cross; dusky marks beside bands (Fig. 359). Black longitudinal band on sides; venter with dusky white transverse patch behind epigynum and white longitudinal band on each side (Fig. 360). Posterior median and lateral eyes 1.2 diameters of anterior medians. Anterior medians 1.4 diameters apart, 1.4 from laterals. Posterior median eyes 0.6 diameter apart, 1.5 from laterals. Abdomen oval (Fig. 359). Total length 2.9 mm. Carapace 1.1 mm long, 0.8 wide. First femur 1.2 mm; patella and tibia 1.5, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.7, fourth 1.2.

Diagnosis. This species differs from *A. bryantae* (Fig. 353) by having the origin of the scape, the anterior end, narrow (Fig. 357).

Natural History. The species was collected in a rain forest, at 2000 m elevation, in Valle Nuevo.

Distribution. Hispaniola (Map 5).

Records. GREATER ANTILLES *Dominican Republic:* Loma Rucilla Mts., Cord. Central, 1600–2600 m, June 1938, 9♀ (P. J. Darlington, MCZ); Valle Nuevo, Cord. Central, Aug. 1938 (P. J. Darlington, MCZ).

Araneus hotteiensis (Bryant)
Figures 361–364, Map 5

Meta hotteiensis Bryant, 1945: 387, fig. 25, ♀. Female holotype from foothills NE of Massif de la Hotte, 1000–1100 m, Haiti, in MCZ, examined. Brignoli, 1983: 230.

Araneus hotteiensis:—Levi, 1986: 105.

Description. Female. Carapace and sternum orange-yellow. Legs orange-yellow with indistinct dusky rings. Dorsum of abdomen dusky with indistinct folium (Fig. 363); sides dusky; venter with median dusky band, sides light, dusky ring around spinnerets (Fig. 364). Posterior median eyes 0.7 diameter of anterior medians, lateral eyes 0.6 diameter. Anterior medians a little less than their diameter apart, 0.8 from laterals. Posterior medians 0.4 their diameter apart, 2 from laterals. Abdomen oval, longer than wide (Fig. 363). Total length 4.1 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.7 mm, patella and tibia 2.2, metatarsus 1.5, tarsus 0.6. Second patella and tibia 1.8 mm, third 0.9, fourth 1.6.

Diagnosis. The posterior rim of the openings of the epigynum in ventral view (Fig. 361) separates this species from *A. hispaniola* (Fig. 366) and *A. elizabethae* (Fig. 358).

Araneus hispaniola (Bryant)
Figures 365–368; Map 5

Aranea hispaniola Bryant, 1945: 366, fig. 2, ♀. Female holotype from Kenscoff, 4300 ft [1300 m], Haiti, in MCZ, examined.

Araneus hispaniola:—Brignoli, 1983: 262.

Description. Female. Carapace light orange, head mottled dusky. Sternum black; coxae light orange. Legs spotted black on orange. Dorsum of abdomen mottled dusky on white, with indistinct outline of folium (Fig. 367). Venter with black area enclosing a pair of anterior light spots; a light band on each side (Fig. 368). Eyes sub-

equal. Anterior medians their diameter apart, their diameter from laterals. Posterior medians 0.7 diameter apart, 2 from laterals. Abdomen oval, longer than wide. Total length 5.0 mm. Carapace 1.7 mm long, 1.6 wide. First femur 2.2 mm, patella and tibia 3.1, metatarsus 2.4, tarsus 1.0. Second patella and tibia 2.7 mm, third 1.4, fourth 2.3.

Note. The description and illustrations were made from a specimen from Kenscoff, Haiti, not a type.

Diagnosis. This species is distinguished from *A. bryantae* (Figs. 353, 354), which has orange legs, by its spotted legs and the shape of the openings of the epigynum on each side of the scape (Fig. 36).

Distribution. Hispaniola (Map 5).

Records. GREATER ANTILLES *Dominican Republic:* San José de las Matas, 450 m, June 1938, ♀ (P. J. Darlington, MCZ). HAITI Kenscoff, 1500–2100 m, Sept. 1934, ♀ (P. J. Darlington, MCZ) (a paratype of *Eustala perdita* Bryant).

Araneus faxoni (Bryant)
Figures 369–371; Map 5

Aranea faxoni Bryant, 1940: 334, figs. 102, 103, ♀. Female holotype from Siboney, Cuba, in MCZ, examined.
Araneus faxoni:—Brignoli, 1983: 262.

Description. Female holotype faded pale yellow-white. Posterior median and lateral eyes 1.5 diameters of anterior medians. Anterior median eyes their diameter apart, their diameter from laterals. Abdomen as wide as long, with anterior humps (Fig. 371). Total length 2.5 mm. Carapace 0.9 mm long, 0.9 wide. First femur 1.1 mm, patella and tibia 1.4, metatarsus 0.8, tarsus 0.4. Second patella and tibia 1.2 mm, third 0.8, fourth 1.1.

Diagnosis. This female is distinguished by a round scape and a small opening on each side of the base of the epigynum (Fig. 369); the abdomen is shield-shaped (Fig. 371).

Araneus bimini new species
Figures 372–375; Map 5

Holotype. Female holotype from Bennetts Harbour, Cat Island, Bahama Islands, 24 Mar. 1953 (E. B. Hayden no. 236), in AMNH. The specific name is a noun in apposition after a collecting locality.

Description. Female holotype. Carapace yellowish, without black eye rings. Sternum and legs yellowish. Dorsum of abdomen with greenish cast and white pigment spots (Fig. 374); venter with white pigment spots. Eyes subequal. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes 0.5 their diameter apart, 2 from laterals. Total length 3.8 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.3 mm, patella and tibia 1.6, metatarsus 1.1, tarsus 0.5. Second pa-

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Figures 353–356. *Araneus bryantae* Brignoli, female. 353. Ventral. 354. Posterior. 355. Dorsal. 356. Abdomen, ventral.

Figures 357–360. *A. elizabethae* new name, female. 357. Epigynum, ventral. 358. Epigynum posterior. 359. Dorsal. 360. Abdomen, ventral.

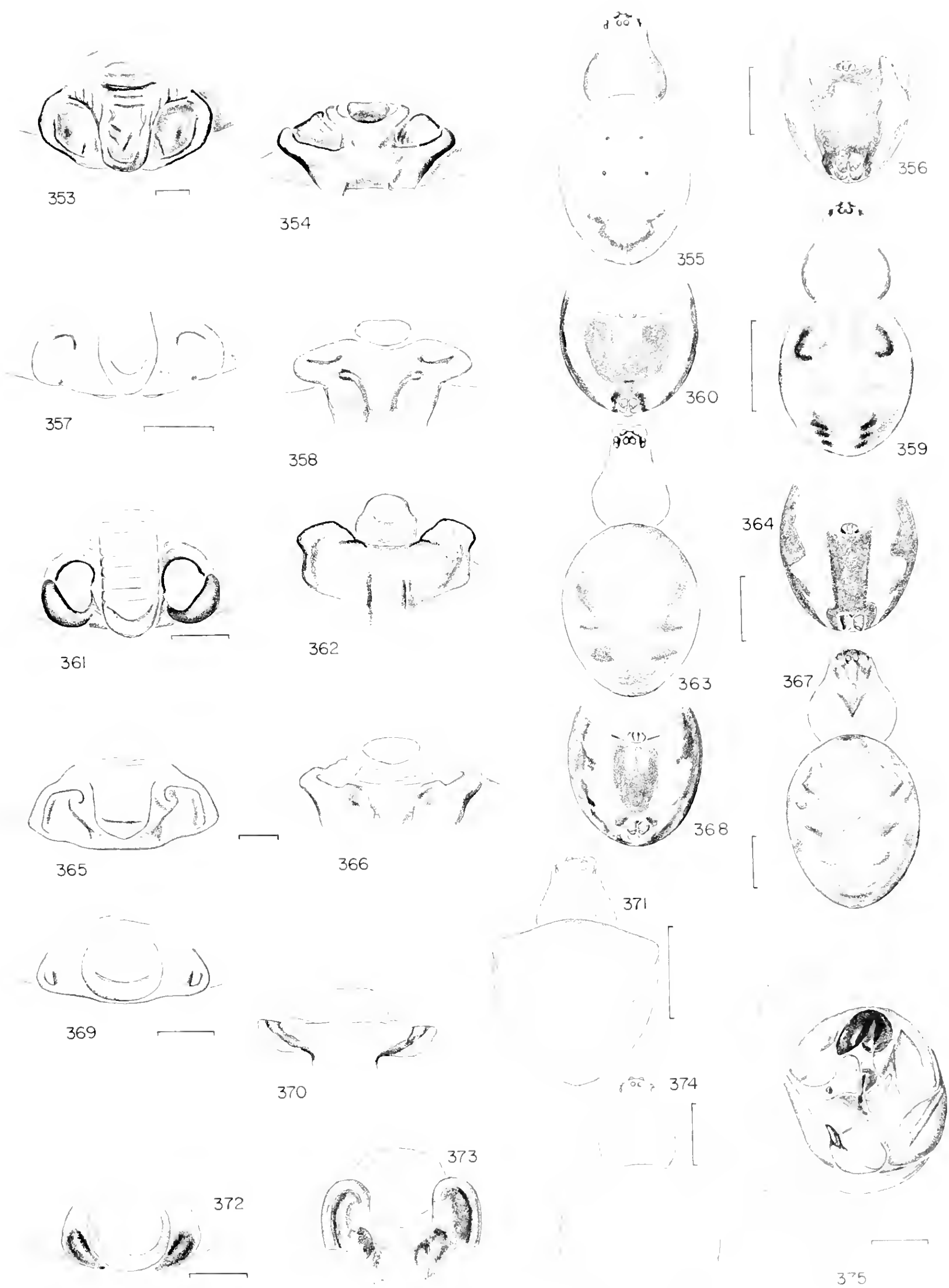
Figures 361–364 *A. hotteiensis* (Bryant), female. 361. Epigynum, ventral. 362. Epigynum, posterior. 363. Dorsal. 364. Abdomen, ventral.

Figures 365–368. *A. hispaniola* (Bryant), female. 365. Epigynum, ventral. 366. Epigynum, posterior. 367. Female. 368. Abdomen, ventral.

Figures 369–371 *A. faxoni* (Bryant) female. 369. Epigynum, ventral. 370. Epigynum, posterior. 371. Dorsal.

Figures 372–375 *A. bimini* n. sp. 372–374. Female. 372. Epigynum, ventral. 373. Epigynum, posterior. 374. Dorsal. 375. Male left palpus

Scale lines. 1.0 mm, genitalia 0.1 mm.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tella and tibia 1.4 mm, third 0.9, fourth 1.3.

Male from Six Hill Cays. Coloration as in female. Secondary eyes 0.7 diameter of anterior medians. Anterior median eyes their diameter apart, 0.8 from laterals. Posterior median eyes 0.8 diameter apart, 2 from laterals. First coxa without hook. Second tibia thinner than first. Abdomen oval, longer than wide. Total length 2.4 mm. Carapace 1.2 mm long, 1.1 wide. First femur 1.5 mm, patella and tibia 1.7, metatarsus 1.3, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.8, fourth 1.2.

Variation. Total length of females 3.3 to 3.8 mm, of males 2.2 to 2.4.

Diagnosis. Unlike that of similar species, the round scape is wider than the portion of the base of the epigynum showing on either side and the opening is hidden by the scape (Figs. 372, 373). The embolus of the palpus is hidden by a lobe of the hematodocha and the conductor (Fig. 375). The species is close to *A. kerr* Levi (1981: 254, figs. 1–4).

Distribution. Bahama Islands (Map 5).

Paratypes. BAHAMA ISLANDS Driggs Hill by South Bight, Andros Isl., 27 Apr. 1953, ♀, ♂ (Hayden, Giovannoli, AMNH); Pine Ridge, Grand Bahama Isl., 13 May 1953, ♂ (E. B. Hayden, AMNH); W end, hotel, Grand Bahama Isl., 3, 4 Mar. 1967, ♀, ♂ (A. M. Nadler, AMNH); South Bimini, May 1951, 2♀, 3♂ (W. J. Gertsch, M. A. Cazier, AMNH, MCZ); Hopetown, Elbow Cay, Great Abaco Isl., June 1951, ♂ (W. G. Hassler, AMNH); Six Hill Cays, off South Caicos Isl., 12 Feb. 1953, ♂ (G. B. Rabb, AMNH).

Araneus colima new species
Figures 376–380; Map 5

Holotype. Female holotype and six female and one male paratypes from Valle Verde, Colima, Mexico, 1 Aug. 1954 (W. J. Gertsch), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange. Sternum brown. Coxae, legs orange. Dorsum of abdomen gray with paired white patches (Fig. 378); venter black with a white longitudinal band on each side almost to spinnerets (Fig. 379). Posterior median eyes 1.6 diameters of anterior median eyes, anterior laterals 1 diameter, posterior laterals 1.1. Anterior median eyes 1.5 diameters apart, 2 from laterals; posterior median eyes 0.5 diameter apart, 2.5 from laterals. Abdomen oval. Total length 3.7 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.1 mm, patella and tibia 1.3, metatarsus 0.7, tarsus 0.5. Second patella and tibia 1.1 mm, third 0.7, fourth 1.1.

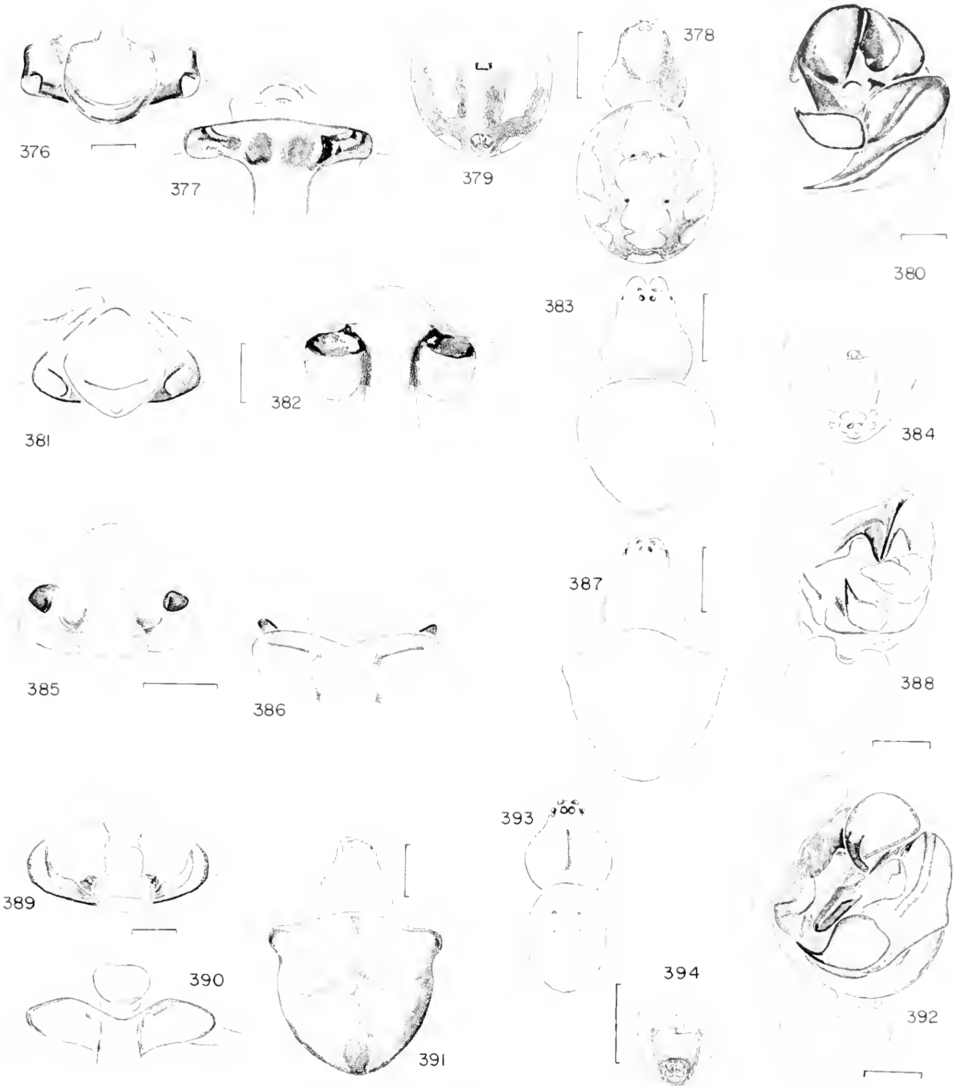
Male. Coloration same as in female, but white areas on abdomen less discrete. Posterior median eyes subequal, anterior lateral eyes 0.8 diameter of anterior median eyes, posterior lateral eyes 0.6. Anterior median eyes their diameter apart, 1.5 from laterals. Posterior median eyes 0.5 diameter apart, 2.2 from laterals. Endite with tooth. First coxa without hook. First tibia thicker than second, with macrosetae. Abdomen oval, longer than wide. Total length 2.7 mm. Carapace 1.4 mm long, 1.2 wide. First femur 1.3 mm, patella and tibia 1.5, metatarsus 0.4, tarsus 0.5. Second patella and tibia 1.2 mm, third 0.7, fourth 1.1.

Variation. Several females have the scape torn off the epigynum. Total length of females 3.1 to 4.0 mm, of males 2.7 to 3.3. One specimen has the scape narrower than in the other females. Some specimens are dark colored.

Diagnosis. The round scape has a stalk and the openings of the epigynum are smaller (Fig. 376) than those of *A. lanio* (Figs. 381, 382). The male is distinguished from others by an almost rectangular median apophysis drawn out to a spine facing the cymbium (Fig. 380).

Distribution. West coast of Central Mexico (Map 5).

Paratypes. MEXICO *Sinaloa:* 3.2 km S Elota, 11 Sept. 1966, ♂ (J., W. Ivie, AMNH); Villa Unión, 30 July 1953, ♀ (N. L. H. Kraus, AMNH); 13 km E Villa Unión, 26 Aug. 1965, 2♂ (W. J. Gertsch, R. Hastings, AMNH). *Nayarit:* 9 km E San Blas, 31 July 1967, ♂ (R. E. Leech, REL); vicinity of San Blas, common (AMNH); Jalisco, 27 July



Figures 376–380. *Araneus colima* n. sp. 376–379. Female. 376. Epigynum, ventral. 377. Epigynum, posterior. 378. Dorsal. 379. Abdomen, ventral. 380. Male, left palpus.

Figures 381–384. *A. lanio* n. sp., female. 381. Epigynum, ventral. 382. Epigynum, posterior. 383. Dorsal. 384. Abdomen, ventral.

Figures 385–388. *A. boneti* n. sp. 385–387. Female. 385. Epigynum, ventral. 386. Epigynum, posterior. 387. Dorsal. 388. Male palpus.

Figures 389–391. *A. ana* n. sp., female. 389. Epigynum, ventral. 390. Epigynum, posterior. 391. Dorsal.

Figures 392–394. *A. jalisco* n. sp., male. 392. Palpus. 393. Dorsal. 394. Abdomen, ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.

1954, ♀ (W. J. Gertsch, AMNH); 32 km N Tepic, 5 Aug. 1956, 10♀, 5♂, 3 imm. (W. J. Gertsch, V. Roth, AMNH). *Jalisco:* Puerto Vallarta, Aug., Sept. 1957, 5♀, ♂ (J. A. Comstock, AMNH); across river from Colima, 29 Aug. 1965, ♂ (W. J. Gertsch, R. Hastings, AMNH). *Colima:* Las Humedades, Armería, 19 Jan., 1943, ♀, ♂ (F. Bonet, AMNH); Armería, 1 Aug. 1954, 2♀, 14♂ (W. J. Gertsch, AMNH); Cuyutlán, 9 Jan. 1943, ♀, ♂ (F. Bonet, AMNH); Valle Verde, 1 Aug. 1954, ♂ (W. J. Gertsch, AMNH).

Araneus lanio new species
Figures 381–384; Map 5

Holotype. Female from 27 km SW of Valle Nacional on Hwy. 175, ca. 1200 m elevation, Oaxaca, Mexico, 24 June 1983 (W. Maddison 83-084), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female. Carapace, sternum, legs light orange-yellow. Dorsum of abdomen white; venter with white square (Fig. 384). Eyes small and subequal. Anterior medians 2 diameters apart, 4 from laterals. Posterior medians a little less than 2 diameters apart, a little less than 4 from laterals. Abdomen as wide as long, pointed behind (Fig. 383). Total length 3.6 mm. Carapace 1.6 mm long, 1.4 wide. First femur 1.4 mm, patella and tibia 1.7, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.7 mm, third 1.1, fourth 1.5.

Diagnosis. This female differs from *A. colima* (Figs. 376, 377) by having a smaller base of the epigynum, with larger openings and the scape broadly attached (Fig. 381).

Araneus boneti new species
Figures 385–388; Map 5

Holotype. Female holotype and male paratype from Santiago, Colima, Mexico, 14 Jan. 1943 (F. Bonet), in AMNH. The species is named after the collector.

Description. Female. Carapace and sternum orange-white; no black around eyes. Legs orange-white. Dorsum and sides of abdomen covered with small white pigment spots; venter without pigment in center. Posterior median eyes same diameter as anterior medians, lateral eyes 0.8 diameter. Anterior median eyes 1.8 diameters apart, 1.8 from laterals. Posterior median eyes 1.5 diameters apart, 2.5 from laterals. Abdomen shield-shaped, slightly wider than long (Fig. 387). Total length 3.8 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.9 mm, patella and tibia 2.2, metatarsus 1.6, tarsus 0.6. Second patella and tibia 1.8 mm, third 1.0, fourth 1.6.

Male. Coloration as in female. Posterior median eyes 0.8 diameter of anterior medians, lateral eyes 0.7 diameter. Anterior median eyes a little less than 2 diameters apart, 1.5 from laterals. Posterior median eyes 1.5 diameters apart, 1.7 from laterals. Palpus with two patellar setae on one side, three on other. Endite with tooth. First coxa without hook. Second tibia as thick as first; no modified tibiae. Abdomen oval, longer than wide, pointed behind, without humps. Total length 2.1 mm. Carapace 1.1 mm long, 0.9 wide. First femur 1.8 mm, patella and tibia 1.9, metatarsus 1.4, tarsus 0.5. Second patella and tibia 1.5 mm, third 0.7, fourth 1.3.

Note. The embolus appears torn out of the male palpus. The conductor lacks a tooth at its base.

Diagnosis. The palpal tibia is as long as wide. The female has a narrower scape than the female of *A. mazamitla* (Fig. 400) and the slits on each side of the scape are shorter (Fig. 385). The male has the palpal tibia as wide as long and has a short, pointed median apophysis and a narrow terminal apophysis (Fig. 388).

Araneus ana new species
Figures 389–391; Map 5

Holotype. Female from 10 km W of Santa Ana, San José Prov., Costa Rica, 800 m, Nov. 1983 (W. Eberhard), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace and sternum light yellow, no black pigment

around eyes. Legs light yellow. Dorsum of abdomen dusky with four white patches (Fig. 391); venter white. Eyes small and subequal. Anterior median eyes 2 diameters apart, 2 from laterals. Posterior median eyes a little more than their diameter apart, a little over 2 from laterals. Abdomen with pair of dorsal humps (Fig. 391). Total length 4.4 mm. Carapace 1.6 mm long, 1.3 wide. First femur 2.0 mm, patella and tibia 2.2, metatarsus 1.7, tarsus 0.7. Second patella and tibia 1.8 mm, third 1.0, fourth 1.6.

Diagnosis. This species is distinguished from others by the epigynum, which in ventral view has a transverse lip on each side of the scape (Fig. 389), and in posterior view has the sclerites fused (Fig. 390).

Araneus jalisco new species
Figures 392–394; Map 5

Holotype. Male from Guadalajara, Jalisco, Mexico, 1 Aug. 1947 (C. Goodnight, B. Malkin), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace light orange with a median dusky line. Sternum dusky with margin black. Legs light orange. Dorsum of abdomen white (Fig. 393); venter with a wide black band from genital groove and surrounding spinnerets; enclosing two indistinct white patches side by side; dusky in middle of epigastric area (Fig. 394). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes their diameter apart, 0.5 from laterals. Posterior medians 0.5 diameter apart, a little less than 2 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first; first with macrosetae. Abdomen oval, longer than wide (Fig. 393). Total length 2.5 mm. Carapace 1.4 mm long, 1.1 wide. First femur 1.4 mm, patella and tibia 1.9, metatarsus 1.4, tarsus 0.6. Second patella and tibia 1.6 mm, third 0.8, fourth 1.5.

Diagnosis. This male differs from others by having a looped embolus above the pear-shaped median apophysis (Fig. 392). There is a tooth at the base of the conductor.

Araneus detrimentosus (O. P.-Cambridge)
Figures 395–399; Map 5

Epeira detrimentosa O. P.-Cambridge, 1889, 1: 26, pl. 6, fig. 8, ♀. Female lectotype designated by Levi, 1973, from between Petab [?] and Chicoyoito [?Chicoyoj] and Chilascó, Guatemala, in BMNH, examined. Keyserling, 1892, 4: 137, pl. 7, fig. 101, ♀.

Epeira nigrohumeralis O. P.-Cambridge, 1893, 1: 111, pl. 15, fig. 3, ♀. Female holotype from Venta de Zopilote [?], 2800 ft, Mexico, in BMNH.

Aranea detrimentosa:—Roewer, 1942: 542.

Aranea vesta Bryant, 1948: 60, figs. 4, 6, ♀, ♂. Female holotype from Acapulco, Mexico, in MCZ, examined. NEW SYNONYMY.

Cambridgepeira detrimentosa:—Archer, 1951b: 2, figs. 8, 9.

Araneus detrimentosus:—Bonnet, 1955: 486. Levi, 1973: 538, figs. 398–414, ♀, ♂.

Description. Female from Mexico. Carapace orange with white down; sternum orange with white pigment. Legs orange, ringed dark. Dorsum of abdomen with brownish-black patches and white line on each side anteriorly, and pairs of dark spots posteriorly (Fig. 397). Venter with paired white spots (Fig. 398). High thorax. Eyes subequal. Anterior median eyes 2 diameters apart, a little less than 2 from laterals. Posterior medians their diameter apart, 2.5 from laterals. Abdomen oval, wider than long (Fig. 397). Total length 5.5 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.4 mm, patella and tibia 2.7, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.3 mm, third 1.2, fourth 1.9.

Male from Mexico. Coloration darker than in female. Dorsum of abdomen white with dark spots. Eyes subequal. Anterior median eyes 1.5 diameters apart, a little less than their diameter from laterals. Posterior medians their diameter apart, 2 from laterals. Endite with tooth. First coxa with hook. Second tibia not swollen. Total length 2.5 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.7 mm, patella and tibia 2.1, metatarsus 1.2, tarsus 0.7. Second patella and tibia 1.5 mm, third 0.9, fourth 1.2.

Variation. Total length of females 4.0 to 6.5 mm, of males 2.3 to 3.4.

Diagnosis. The epigynum has a scape that may widen toward the tip; the openings are behind a slit on each side of the scape (Fig. 395). In posterior view the median and lateral plates are fused into a single shield which projects ventrally on each side (Fig. 396). The male palpus has a curved embolus seen just above the median apophysis (Fig. 399). The median apophysis has just one spine, which projects away from the bulb (Fig. 399). Unlike most other small *Araneus* species, the male has a coxal hook.

Natural History. The species has been collected from a seasonal tropical forest in Yucatan.

Distribution. From Gulf coast in Florida to Texas and California to northern Colombia along coast and elsewhere, usually at low elevations (Map 5).

Additional Records. MEXICO *Tamaulipas:* San José (MCZ); 16 km S Reynosa (AMNH); 50 km S Reynosa (CAS). *Nuevo León:* Villagrán (AMNH). *Sonora:* Estero de Sargente, 20 km S Desemboque (AMNH); Desemboque (AMNH). *Durango:* San Juan del Río (AMNH); El Táscate (AMNH). *Sinaloa:* 67 km E Villa Unión, 1500 m (AMNH); 57 km E Villa Unión (AMNH); Mazatlan (AMNH, CAS, MCZ). *Nayarit:* San Blas (UCR); 8 km NW Tepic (AMNH). *Jalisco:* 5 km N Guanajuato (AMNH); 90 km N Playa de Santiago (CAS). *Colima:* Manzanillo (MCZ). *Veracruz:* Veracruz (AMNH, CAS, MCZ); nr. Lago Catemaco (AMNH); Jalapa (MCZ). *Guerrero:* Puerto Marquez (AMNH); Revolcadero (AMNH); Acapulco (AMNH, MCZ); 51 km SE Petatlán (MCZ). *Oaxaca:* Playa Hati, Río Tonto (MCZ); Huajuapan (MCZ); San Gerónimo (MCZ). *Yucatan:* 4 km N Xocempich, 20°47′N, 88°34′W (MCZ). *Chiapas:* Cintalapa (MCZ). GUATEMALA; San Jerónimo (AMNH). COSTA RICA *Guanacaste:* Monteverde (MZC). PANAMA *Chiriquí:* Boquete (AMNH, MCZ). *Coclé:* El Valle (AMNH). *Panamá:* Isl. Taboga (AMNH); Fort Kobbe (MCZ); Forest Reserve (MCZ). COLOMBIA *Magdalena:* Gaira, 10 m (MCZ).

Araneus mazamitla new species
Figures 400–403; Map 5

Holotype. Female holotype and four female, two male and two immature paratypes from 240 km E of Mazamitla, Colima, Mexico, 2 Aug. 1956 (W. J. Gertsch, V. Roth), in AMNH. The specific name is a noun in apposition after the type locality.

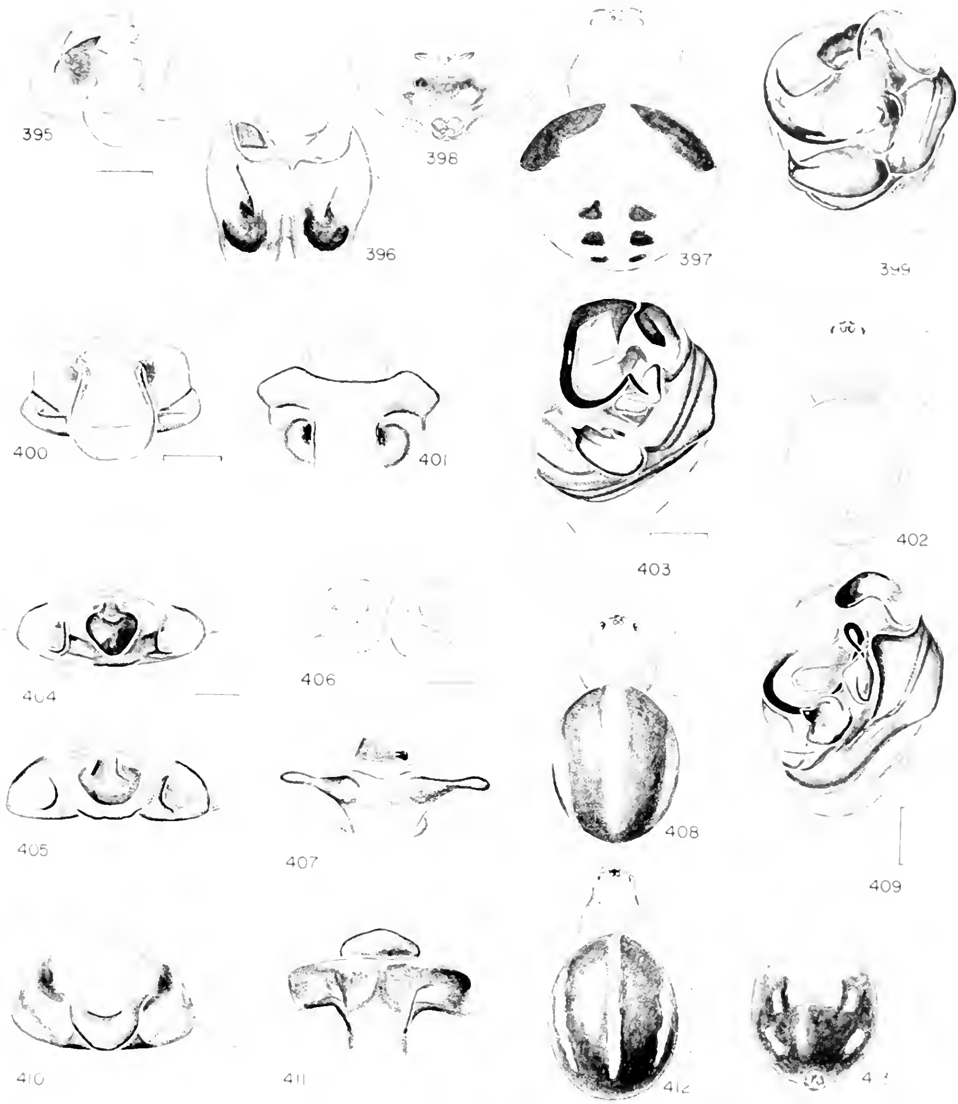
Description. Female. Carapace and sternum orange. Legs orange, distal articles dusky. Dorsum of abdomen lighter orange with three white longitudinal pigment lines (Fig. 402); venter orange. Posterior median eyes 1.2 diameters of anterior medians, laterals 1 diameter. Anterior median eyes a little less than their diameter apart, a little less than 2 from laterals. Posterior median eyes 0.6 their diameter apart, 2 from laterals. Abdomen oval. Total length 3.0 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.3 mm, patella and tibia 1.4, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.2 mm, third 0.8, fourth 1.3.

Male paratype. Color as in female. Eyes as in female. Endite with tooth. First coxa without hook. First tibia thicker than second and with larger macrosetae. Abdomen oval. Total length 2.6 mm. Carapace 1.4 mm long, 1.1 wide. First femur 1.4 mm, patella and tibia 1.5, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.2 mm, third 0.8, fourth 1.3.

Variation. Total length of males 2.2 to 2.6 mm.

Diagnosis. The female differs from *A. flavus* (Figs. 404–407) and *A. tepic* (Figs. 410, 411) by having the openings of the epigynum behind a transverse slit on each side of the scape, and by having the proximal end of the scape narrow (Fig. 400). The male is distinguished by the coiled shape of the embolus, which hangs from the "top" of the bulb (Fig. 403).

Paratypes: MEXICO *Jalisco:* Chamela, 100 m, Sept. 1988, 4♀, 3♂ (W. Eberhard, MCZ). *Colima:* Armería, 1 Aug. 1954, ♀, 2 imm. (W. J. Gertsch, AMNH). *Guerrero:* Acapulco, 17 June 1936, ♂ (L. I. Davis, AMNH).



Figures 395–399. *Araneus detrimentosus* (O. P.-Cambridge). 395–398. Female. 395. Epigynum, ventral. 396. Epigynum, posterior. 397. Dorsal. 398. Abdomen, ventral. 399. Male, left palpus.

Figures 400–403. *A. mazamitla* n. sp. 400–402. Female. 400. Epigynum, ventral. 401. Epigynum, posterior. 402. Dorsal. 403. Male palpus.

Figures 404–409. *A. flavus* (O. P.-Cambridge). 404–408. Female. 404. Epigynum, ventral. 405. Epigynum, venter with torn-off scape. 406. Epigynum, cleared. 407. Epigynum, posterior. 408. Dorsal. 409. Male palpus.

Figures 410–413. *A. tepic* n. sp., female. 410. Epigynum, ventral. 411. Epigynum, posterior. 412. Dorsal. 413. Abdomen, ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.

Araneus flavus (O. P.-Cambridge)
Figures 404–409; Map 5

Singa flava O. P.-Cambridge, 1894: 136, pl. 17, fig. 15, ♂. Male holotype from Tierra Colorada, Guerrero, Mexico, on the road from Chilpancingo to Acapulco, 2000 ft [600 m], in BMNH, examined. Roewer, 1942: 877.
Aranea flava (F. P.-Cambridge), 1904: 518, pl. 51, fig. 3, ♂ (not *Epeira flava* Giebel, 1867).
Araneus flavus:—Bonnet, 1955: 504.

Note. The male holotype is on a pin in alcohol and lacks legs. O. P.-Cambridge described the species and named it *flava* but the legend to the plate is *lutea*. F. P.-Cambridge put legend and description together.

Description. Female from Nicaragua. Carapace glabrous, orange, with black around eyes; sternum orange. Legs orange, dusky dorsally. Dorsum of abdomen glabrous, black with three orange bands (Fig. 408); venter black with orange areas on each side. Posterior median eyes 1.3 diameters of anterior medians, anterior lateral eyes same diameter as anterior medians, posterior lateral eyes 1.1 diameters of anterior medians. Anterior median eyes 1.2 diameters apart, 2.2 from laterals. Posterior median eyes a little less than their diameter apart, 3 from laterals. Abdomen oval (Fig. 408). Total length 3.5 mm. Carapace 1.6 mm long, 1.2 wide. First femur 1.3 mm, patella and tibia 1.5, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.8, fourth 1.3.

Male from Chiapas. Much lighter than female, with indistinct abdominal markings: white pigment spots in three lines on light background. Eyes small and subequal. Anterior median eyes 2 diameters apart, 2 from laterals. Posterior median eyes 1.5 diameters apart, 3 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first. Total length 2.5 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.3 mm, patella and tibia 1.4, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.8, fourth 1.2.

Variation. Total length of females 3.0 to 3.5 mm, of males 2.3 to 3.1.

Diagnosis. The markings on the abdomen (Fig. 408) are shared only with *A. pratensis* (Emerton) (Levi, 1973: 492, figs. 21–31) of the eastern United States and *A. mazamitla* and *A. tepic* (Fig. 412). Females of *A. flavus* are distinguished from these by the stalked scape (Fig. 404); males have a longer embolus than *A. mazamitla* (Fig. 403) has, originating from near the middle of the bulb (Fig. 409).

Distribution. Pacific coast from Chiapas, Mexico, to Nicaragua (Map 5).

Records. MEXICO "Managna" [?Managua, Nicaragua], ♀ (MCZ). *Morelos:* 19 km E Cuernavaca, 15 Aug. 1954, ♀ (R. Dreisbach, MCZ). *Chiapas:* Escuintla, 4♀, 2♂ (Crawford, MCZ); La Zacualpa, Aug. 1909, 2♀, 9♂, 7 imm. (A. Petrunkevitch, AMNH); Tonalá, Aug. 1909, ♀ (A. Petrunkevitch, AMNH); Arriaga, N Arriaga Mts., 2 Sept. 1947, ♂ (H. Wagner, AMNH). GUATEMALA Tiquisate, 60 m, 26–29 June 1947, ♂ (C., P. Vaurie, AMNH). NICARAGUA San Marcos, 2♀ (C. F. Baker, MCZ); Volcán Cosiguina, 25 Aug. 1989, ♂ (F. Reinboldt, JMM); Isla de Ometepe, July 1989, ♀ (F. Reinboldt, JMM).

Araneus tepic new species
Figures 410–413; Map 5

Holotype. Female from 24 km N of Tepic, Nayarit, Mexico, 25 July 1954 (W. J. Gertsch), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange with a minute dusky spot on each side of head. Sternum and legs orange. Dorsum of abdomen black with three white lines (Fig. 412). Venter black with two white patches on each side (Fig. 413). Posterior median eyes 1.7 diameters of anterior medians, lateral eyes 1.1 diameters. Anterior medians 1.2 diameters apart, 2.5 from laterals. Posterior medians 0.3 diameter apart, 2.5 from laterals. Abdomen oval (Fig. 412). Total length 3.6 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.2 mm, patella and tibia 1.3, metatarsus 0.8, tarsus 0.4. Second patella and tibia 1.1 mm, third 0.8, fourth 1.2.

Diagnosis. This female differs from *A. flavus* (Figs. 404–407) and *A. mazamitla* (Figs. 400–401) by having the scape of the epigynum short and wide, widest at its attachment (Fig. 410).

Araneus montereyensis (Archer)
Map 5

Conaranea montereyensis Archer, 1951b: 8, figs. 8, 24, 25, ♀, ♂. Female holotype from Monterey, California, in AMNH.
Araneus montereyensis:—Levi, 1973: 506, figs. 108, 109, 138, 151, map 3.

Diagnosis. The female has a straight scape with the openings anterior on each side of the scape as in *A. adjuntaensis* (Fig. 414), but posteriorly the plates are fused into one narrow transverse sclerite (Levi, 1973, figs. 139, 141). The male differs from other species by having the long median apophysis spine directed anteromesally, the frayed end directed anterolaterally (Levi, 1973, figs. 145, 146).

Distribution. California.

Record. MEXICO *Baja California Norte:* 23 km SE Maneadero, 19 May 1965, ♀ (D. Q. Cavagnero, E. S. Ross, CAS).

Araneus adjuntaensis (Petrunkevitch)
Figures 414–417; Map 5

Meta adjuntaensis Petrunkevitch, 1930: 349: figs. 232–234, ♀. Female holotype from Adjuntas, Puerto Rico, collected by sweeping virgin forest, in AMNH, examined. Roewer, 1942: 918.

Description. Female. Carapace orange with black marks (Fig. 416). Chelicerae, labium, endites orange. Sternum black on sides with an orange band in middle. Legs light orange with narrow black rings. Dorsum of abdomen black, gray and white spotted (Fig. 416); venter with black band, white on each side (Fig. 417). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1 diameter apart, 1 from laterals. Posterior median eyes 0.3 diameter apart, 1.3 from laterals. Abdomen damaged. Total length 3.4 mm. Carapace 1.2 mm long, 1.1 wide. First femur 1.7 mm, patella and tibia 1.9, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.0, fourth 1.5.

Diagnosis. This species differs from *A. miniatus* (Levi, 1973: 506, figs. 158–171) found in the southeastern United States by having the oval abdomen longer than wide (Fig. 416) (the abdomen of *A. miniatus* is wider than long). *Araneus adjuntaensis* also has a shorter scape in the epigynum (Fig. 414). In posterior view of the epigynum, the ducts, which show through the sclerites, take a ventral-posterior course (Fig. 415), while those of *A. miniatus* loop in a transverse direction.

Record. PUERTO RICO Toro Negro State Forest, 7 Nov. 1971, ♀ (J. E. Carico, MCZ).

Araneus caballo new species
Figures 418–421; Map 5

Holotype. Female holotype from 11 km SW of Filo de Caballo, Guerrero, Mexico, 12 July 1985 (J. Woolley, G. Zolnerowich), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange with some dark hairs on head. Chelicerae, labium, endites orange. Sternum orange, border dusky. Coxae orange; legs light orange. Dorsum of abdomen white with indistinct paired dark marks (Fig. 420); venter with two longitudinal rectangles on dusky background (Fig. 421). Posterior median eyes 2 diameters of anterior medians, laterals same diameter as anterior medians. Anterior median eyes 2.2 diameters apart, 3.7 from laterals. Posterior median eyes 2 diameters apart, 3 from laterals. Abdomen slightly longer than wide with a pair of rounded humps (Fig. 420). Total length 3.1 mm. Carapace 1.5 mm long, 1.1 wide. First femur 1.7 mm, patella and tibia 2.1, metatarsus 1.2, tarsus 0.5. Second patella and tibia 1.7 mm, third 0.9, fourth 1.5.

Diagnosis. This species differs from *A. montereyensis* (Levi, 1973: 506, figs. 108, 109, 138, 151) and *A. adjuntaensis* (Figs. 414, 415) by lacking the anterior openings on the base of the epigynum (Fig. 418)

and in the shape of the base in posterior view (Fig. 419).

Araneus ubicki new species
Figures 422–426; Map 5

Holotype. Female holotype and one female and one male paratypes from Monteverde, Res. Bosque Nuboso, 1700 m, cloud forest, Puntarenas Prov., Costa Rica, 1–4 Apr. 1983 (D. Ubick), in CAS. This species is named after the collector.

Description. Female. Carapace, chelicerae, labium, endites orange. Sternum dark orange. Coxae orange; legs orange, slightly dusky underneath. Dorsum of abdomen with black marks, a median white pigment stripe, and white pigment on sides (Fig. 424). Venter orange between epigynum and spinnerets, light on sides; sides of abdomen gray (Fig. 425). Posterior median eyes 1.5 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes 1.4 diameters apart, 2.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen oval with indistinct humps (Fig. 424). Total length 3.4 mm. Carapace 1.4 mm long, 1.2 wide. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.4 mm, third 0.9, fourth 1.3.

Male. Color as in female but abdomen lacks white. Posterior median eyes 1.8 diameters of anterior medians, anterior laterals 1.2 diameters, posterior laterals 1. Anterior median eyes 1.5 diameters apart, 2 from laterals. Posterior median eyes 0.9 diameter apart, 2 from laterals. Endite with tooth. First coxa without hook. First tibia thicker than second, with some long macrosetae. Abdomen oval. Total length 2.6 mm. Carapace 1.2 mm long, 1.1 wide. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.4 mm, third 0.8, fourth 1.1.

Diagnosis. The female is distinguished from other species by the epigynum, in which connecting duct loops show in the base on each side of the scape (Figs. 422, 423). The male differs by having the palpal embolus long and slightly curved, and by the presence of a small knob on the median apophysis (Fig. 426).

Araneus musawas new species
Figures 427, 428; Map 5

Holotype. Male from Musawas, Waspuc River [Río Huaspuc], Nicaragua, 30 Sept. 1955 (B. Malkin), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace, sternum and legs orange, sternum slightly dusky. Dorsum of abdomen dusky with a white cardiac mark (Fig. 428); venter dusky. Posterior median eyes 0.7 diameter of anterior medians, lateral eyes 0.6 diameter. Anterior median eyes a little less than their diameter apart, the same from laterals. Posterior median eyes 0.6 diameter apart, 2.5 from laterals. Endite with tooth. First coxa without hook. Legs slender; second

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Figures 414–417. *Araneus adjuntaensis* (Petrunkevitch), female. 414. Epigynum, ventral. 415. Epigynum, posterior. 416. Dorsal. 417. Abdomen, ventral.

Figures 418–421. *A. caballo* n. sp., female. 418. Epigynum, ventral. 419. Epigynum, posterior. 420. Dorsal. 421. Abdomen, ventral.

Figures 422–426. *A. ubicki* n. sp. 422–425. Female. 422. Epigynum, ventral. 423. Epigynum, posterior. 424. Dorsal. 425. Abdomen, ventral. 426. Male, left palpus.

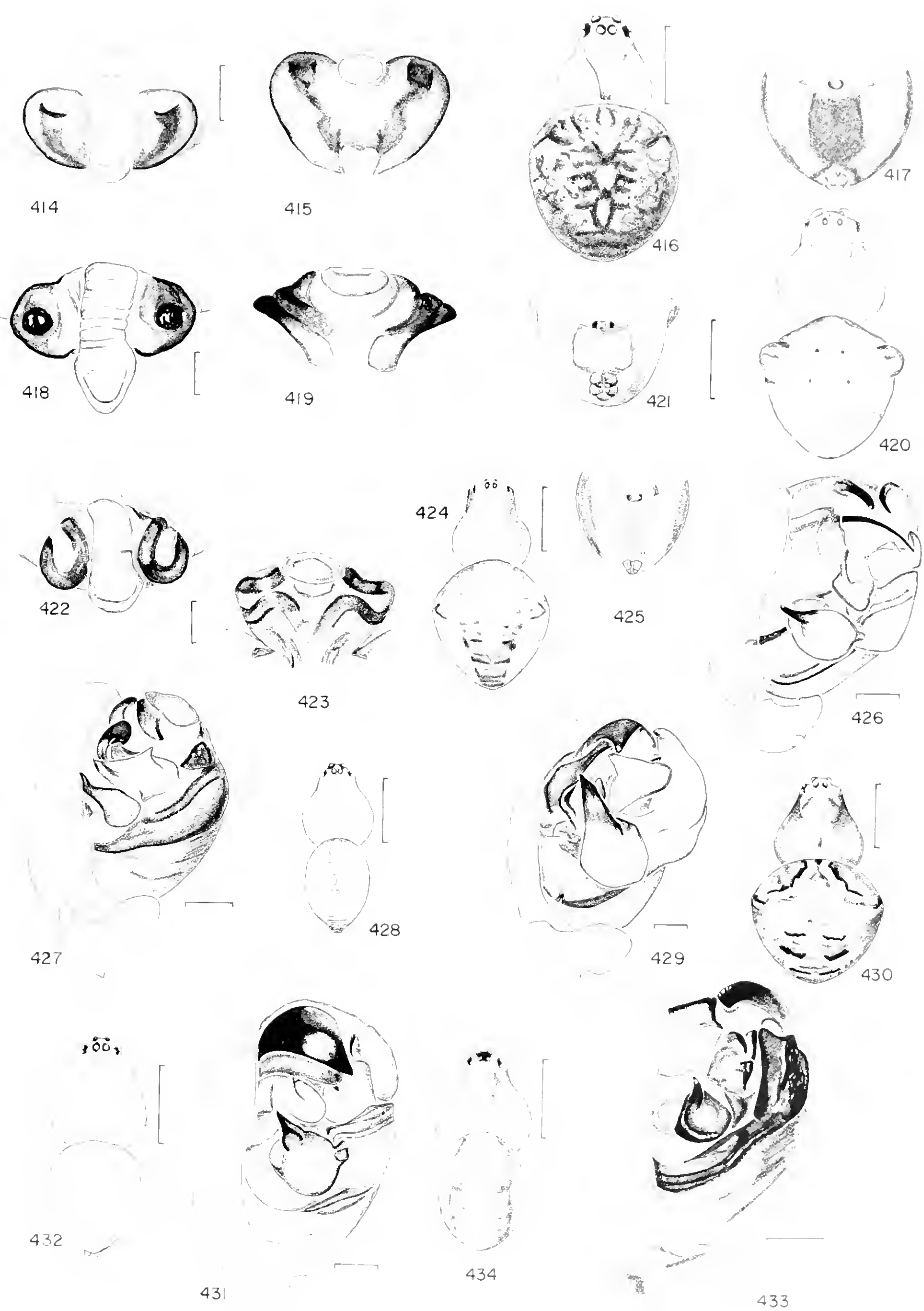
Figures 427, 428. *A. musawas* n. sp., male. 427. Palpus. 428. Dorsal.

Figures 429, 430. *A. frio* n. sp., male. 429. Palpus. 430. Dorsal.

Figures 431, 432. *A. nuboso* n. sp., male. 431. Palpus. 432. Dorsal.

Figures 433, 434. *A. uruapan* n. sp., male. 433. Palpus. 434. Dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.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tibia thinner than first, first with long macrosetae. Abdomen narrow, oval. Total length 2.5 mm. Carapace 1.4 mm long, 1.2 wide. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.9, fourth 1.2.

Diagnosis. This male is distinguished by details of the palpus: the conductor almost touches the cymbium, and hides the coiled embolus (Fig. 427). Also, the spine of the median apophysis is drawn out beyond the edge of the cymbium (Fig. 427).

Araneus frio new species
Figures 429, 430; Map 5

Holotype. Male from W of Río Frío, 3200 m, Distríto Federal, Mexico, 22 Aug. 1964 (J., W. Ivie), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Male. Head orange, sides dusky to black, carapace dusky orange. Sternum black. Coxae light orange; legs with dusky rings on light orange. Dorsum of abdomen with median white chevron anteriorly, dark transverse bars posteriorly. Venter dark with black spots and a pair of white brackets. Posterior median eyes 1.5 diameters of anterior medians, lateral eyes 0.5 diameter. Anterior median eyes 1.5 diameters apart, 1.4 from laterals. Posterior median eyes a little more than their diameter apart, 1.5 from laterals. Endite with tooth. First coxa without hook. Second tibia as thick as first, not modified. Abdomen with distinct humps (Fig. 430). Total length 3.2 mm. Carapace 1.7 mm long, 1.5 wide. First femur 2.0 mm, patella and tibia 2.4, metatarsus 1.5, tarsus 0.6. Second patella and tibia 2.0 mm, third 1.1, fourth 1.4.

Diagnosis. This male is distinguished from others by the large pointed median apophysis and stalked conductor of the palpus (Fig. 429).

Araneus nuboso new species
Figures 431, 432; Map 5

Holotype. Male holotype from Monteverde, Res. Bosque Nuboso, 1700 m, cloud forest, Puntarenas Prov., Costa Rica, 1–4 Apr. 1983 (D. Ubick), in CAS. The specific name is a noun after the type locality.

Description. Male. Carapace yellow-white, a dusky patch on each side of thorax. Chelicerae, labium, endites yellow-white. Sternum light orange. Coxae yellow-white; legs yellow-white, distal articles orange. Dorsum of abdomen with white pigment spots (Fig. 432); venter yellowish without pigment. Posterior median eyes 1.5 diameters of anterior medians, anterior laterals 1.2 diameter, posterior laterals 1. Anterior median eyes 1.4 diameters apart, 1.6 from laterals. Posterior median eyes 1 diameter apart, slightly more than 2 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first; first with some long macrosetae. Abdomen oval. Total length 2.7 mm. Carapace 1.4 mm long, 1.2 wide. First femur 1.5 mm, patella and tibia 1.7, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.5 mm, third 0.8, fourth 1.2.

Diagnosis. The embolus is long and filamentous. Only its tip is visible on the left of the conductor. On top of the conductor hangs a spine attached to the terminal apophysis (Fig. 431).

Araneus uruapan new species
Figures 433, 434; Map 5

Holotype. Male holotype and one male paratype from 16 km S of Uruapan, Michoacan, Mexico, 6 July 1985 (J. Woolley and G. Zolnerowich), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace light orange, dusky on sides of head. Chelicerae, labium, endites orange. Sternum dusky orange. Coxae light orange; legs orange. Dorsum of abdomen with longitudinal dusky line on each side and lines connected by broken transverse bars (Fig. 434); venter dusky. Posterior median eyes 1.3 diameters of anterior medians, laterals same diameter as anterior medians. Anterior median eyes 1.2 diameters apart, 1.3 from laterals. Posterior median eyes 1 diameter apart, 2.5 from laterals. Endite with large

tooth facing large tooth on palpal femur. First coxa without hook. Second tibia thinner than first. Abdomen oval, equally rounded anteriorly and posteriorly (Fig. 434). Total length 2.5 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.3 mm, patella and tibia 1.5, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.9, fourth 1.2.

Diagnosis. The male differs by having the tip of the embolus overhanging the "top" of the conductor, and by having a round median apophysis with an apical spine (Fig. 433).

Araneus cristobal new species
Figures 435–439; Map 5

Holotype. Female holotype and female and male paratypes from Grutas de San Cristóbal, ca. 16 km SE of San Cristóbal, Chiapas, Mexico on Hwy. 190, 27 July 1983, in pine forest (W. Maddison), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Head mottled brown, sides of thorax lighter. Sternum dark brown. Coxae light; legs mottled brown, ringed. Dorsum of abdomen with folium, brown-black with symmetrical white spots and white lines (Fig. 437); venter black with white line on each side, sides brown (Fig. 438). Eyes small and subequal. Anterior median eyes 2 diameters apart, 2.5 from laterals. Posterior median eyes 1.2 diameters apart, 3.5 from laterals. Abdomen diamond-shaped. Total length 4.2 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.7 mm, patella and tibia 2.2, metatarsus 1.3, tarsus 0.5. Second patella and tibia 1.8 mm, third 1.1, fourth 1.6.

Male. Color as in female, but lighter than female illustrated. Posterior median and lateral eyes 0.6 diameter of anterior medians. Anterior median eyes their diameter apart, 1.3 from laterals. Posterior median eyes 1.5 diameters apart, 2.5 from laterals. Endite with tooth. First coxa without hook. First tibia with macrosetae. Second tibia as thick as first. Total length 3.2 mm. Carapace 1.6 mm long, 1.4 wide. First femur 2.0 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.9 mm, third 0.9, fourth 1.4.

Note. Some female paratypes are lighter colored; one of them in the AMNH is dark and has a slightly longer, slightly twisted, and narrower scape.

Diagnosis. The female is distinguished by having an opening in the base on each side of the short stubby scape (Fig. 435), and by the shape of the median and lateral plates (Fig. 436). The male is distinguished by the curved embolus originating from the "top" of the bulb (Fig. 439).

Natural History. Specimens have been collected in oak-pine woodland and on roadside bushes.

Paratypes. MEXICO *Oaxaca:* 23 km SW Valle Nacional, Hwy. 175, 1000 m, 25 June 1983, ♂ (W. Maddison, R. S. Anderson, MCZ). *Chiapas:* 5 km W San Cristóbal de Las Casas, Hwy. 190, 2300 m, 16°44'N, 92°41'W, 27–28 July 1983, ♂ (W. Maddison, R. S. Anderson, MCZ); San Cristóbal de Las Casas, 12 July 1950, ♀ (C., M. Goodnight, L. Stannard, AMNH).

Araneus axacus new species
Figures 440–444; Map 5

Holotype. Female holotype and male and female paratypes from 60 km SW of Valle Nacional on Hwy. 175 near 17.5°N, 96.5°W, 2800 m, Oaxaca, Mexico, 3 Aug. 1983, powerline clearing (W. Maddison), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female. Carapace and sternum orange-brown, sides of head darker. Sternum orange-brown. Coxae yellowish; legs orange-brown. Folium on dorsum of abdomen black posteriorly, outlined by white, with a median white band on brown (Fig. 442); venter black, framed by two parallel white bands edged laterally with brown (Fig. 443). Carapace hirsute. Eyes small and subequal. Anterior median eyes 1.2 diameters apart, a little less than 2 from laterals. Posterior median eyes their diameter apart, 2.2 from laterals. Abdomen with large humps. Total length 4.8 mm. Carapace 2.2 mm long, 1.8 wide. First femur 2.1 mm, patella and tibia

2.5, metatarsus 1.3, tarsus 0.8. Second patella and tibia 2.3 mm, third 1.2, fourth 1.9.

Male. Coloration as in female, except legs indistinctly ringed. Eyes small and subequal. Anterior median eyes 1.2 diameters apart, 1.5 from laterals. Posterior median eyes a little more than 1 diameter apart, 2.2 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first. Abdomen narrower than in female but with similar large humps. Total length 4.2 mm. Carapace 2.2 mm long, 1.7 wide. First femur 2.5 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.5 mm, third 1.3, fourth 2.0.

Variation. The epigynum of the female paratype has the scape more slender than that of the holotype illustrated, and curved back on itself at its base.

Diagnosis. The female differs from that of *A. cristobal* (Figs. 435, 436) by having the median plate of the epigynum extend ventrally and posteriorly (Figs. 440, 441). The male differs from *A. cristobal* by having a short curved embolus visible behind the spine of the median apophysis (Fig. 444).

Araneus cochise Levi
Figures 445–448; Map 5

Araneus cochise Levi, 1973: 497, figs. 55–59, ♀. Female holotype from Southwest Research Station, 1800 m, Chiricahua Mts., Arizona, in AMNH. Brignoli, 1983: 261. Dean, Agnew, and Breene, 1989: 125, figs. 1, 2, ♂.

Description. Female from Zacatecas, Mexico. Carapace light orange, dusky on each side of head. Chelicerae, labium, endites brown. Sternum brown with a light patch anteriorly. Coxae light orange; legs light orange with narrow dusky rings. Dorsum of abdomen covered by white pigment spots and dusky areas, a dark spotty folium posteriorly (Fig. 447). Venter dusky between epigynum and spinnerets, with a white narrow band on each side of dusky area, bordered by a fine dusky line. Posterior median eyes 1.2 diameters of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.6. Anterior median eyes their diameter apart, 2 from laterals. Posterior median eyes 0.8 their diameter apart, 2.2 from laterals. Abdomen wider than long with distinct, rounded humps. Total length 4.7 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.9 mm, patella and tibia 2.1, metatarsus 1.2, tarsus 0.5. Second patella and tibia 1.9 mm, third 1.1, fourth 1.6.

Male from Texas. Coloration light yellowish as in female. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1.2 diameters apart, 1.2 from laterals. Posterior median eyes their diameter apart, 2 from laterals. Endite with tooth. First coxa without hook. First tibia thicker than second with some long macrosetae. Abdomen oval. Total length 2.9 mm. Carapace 1.6 mm long, 1.5 wide. First femur 1.7 mm, patella and tibia

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Figures 435–439. *Araneus cristobal* n. sp. 435–438. Female. 435. Epigynum, ventral. 436. Epigynum, posterior. 437. Dorsal. 438. Abdomen, ventral. 439. Male, left palpus.

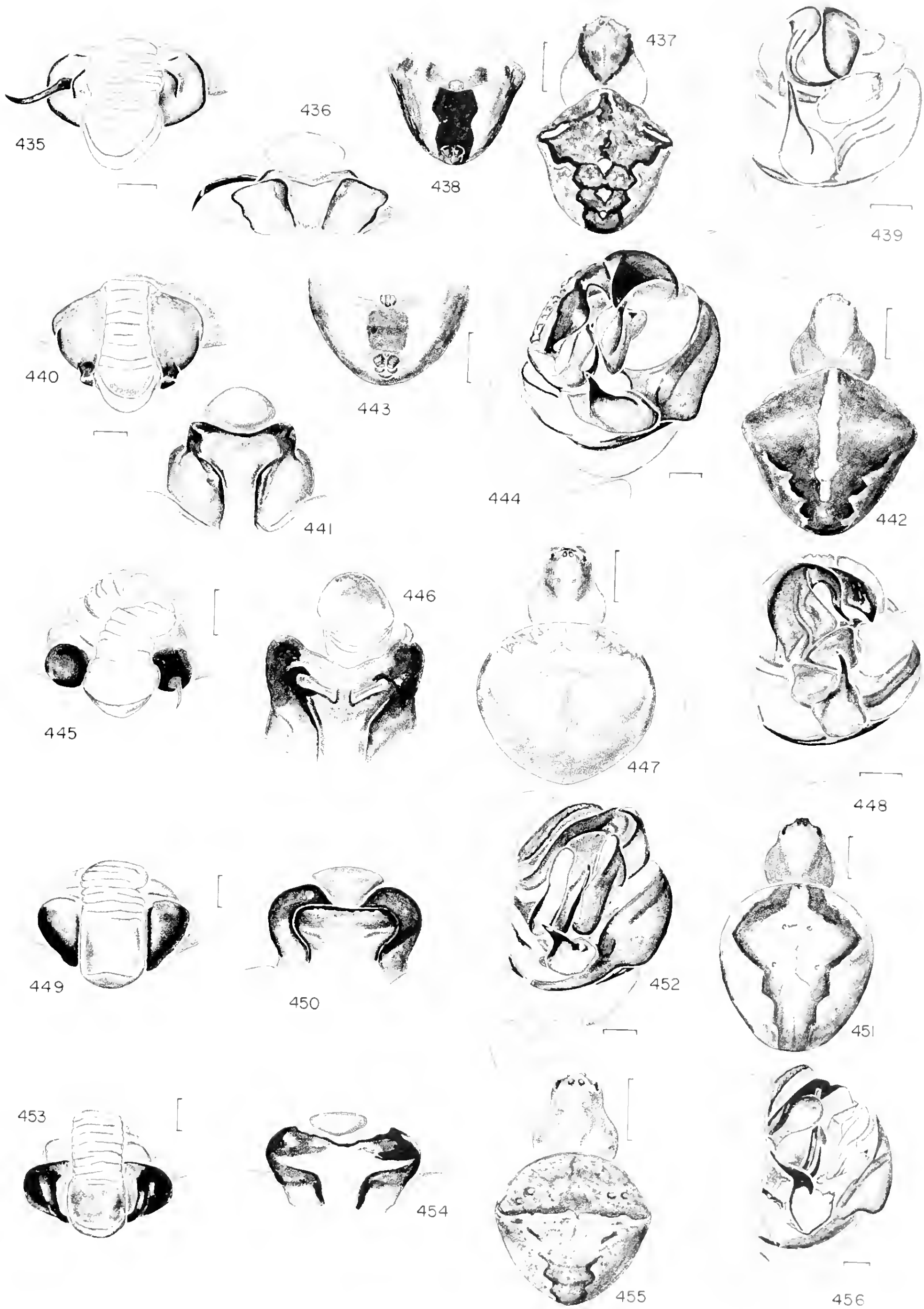
Figures 440–444. *A. axacus* n. sp. 440–443. Female. 440. Epigynum, ventral. 441. Epigynum, posterior. 442. Dorsal. 443. Abdomen, ventral. 444. Male palpus.

Figures 445–448. *A. cochise* Levi. 445, 446. Female. 445. Epigynum, ventral. 446. Epigynum, posterior. 447. Dorsal. 448. Male palpus.

Figures 449–452. *A. dreisbachi* n. sp. 449–451. Female. 449. Epigynum, ventral. 450. Epigynum, posterior. 451. Dorsal. 452. Male palpus.

Figures 453–456. *A. desierto* n. sp. 453–455. Female. 453. Epigynum, ventral. 454. Epigynum, posterior. 455. Dorsal. 456. Male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.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1.9, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.7 mm, third 0.9, fourth 1.3.

Variation. Total length of females 3.4 to 4.5 mm.

Diagnosis. The female differs from other species by having a pair of heavily sclerotized spheres, one on each side of the scape of the epigynum (Fig. 445). The abdomen has rounded humps (Fig. 447). The male has only one long spine on the median apophysis and the embolus makes a clockwise loop (in the left palp), the duct showing through its thicker base (Fig. 448).

Natural History. Females were collected by beating *Acacia* trees in Zacatecas.

Distribution. From Arizona, Texas to Zacatecas, Mexico (Map 5).

Additional Records. TEXAS (Dean et al., 1989). MEXICO *Chihuahua:* 8 km E Parral, 15 July 1947, ♀ (W. J. Gertsch, AMNH). *Durango:* Palos Colorados, 5 Aug. 1947, 2♀ (W. J. Gertsch, AMNH); El Táscate, 27 July 1947, 4♀ (W. J. Gertsch, AMNH). *Zacatecas:* 11 km SE Salinas, on Hwy. 49, 2160 m, 22°34'N, 101°39'W, 8 Aug. 1983, 2 ♀ (W. Maddison, MCZ).

Araneus dreisbachi new species
Figures 449–452; Map 5

Holotype. Female holotype and two male paratypes from Volcán Popocatepetl, 3800 m, Est. México, Mexico (R. Dreisbach), in MCZ. The species is named after the collector.

Description. Female. Carapace, sternum, and legs orange-brown. Coxae orange. Dorsum of abdomen contrastingly marked with folium (Fig. 451); venter blackish with pair of longitudinal lines consisting of white pigment spots. Eyes subequal. Anterior median eyes 2 diameters apart, 2.2 from laterals. Posterior medians their diameter apart, 3 from laterals. Abdomen oval, with slight shoulder humps (Fig. 451). Total length 5.6 mm. Carapace 2.2 mm long, 1.9 wide. First femur 2.1 mm, patella and tibia 2.6, metatarsus 1.6, tarsus 0.8. Second patella and tibia 2.3 mm, third 1.3, fourth 2.0.

Male. Color as in female. Posterior median and lateral eyes 0.9 diameter of anterior medians. Anterior median eyes 1.5 diameters apart, 1.7 from laterals. Posterior median eyes their diameter apart, a little over 2 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first. Total length 3.8 mm. Carapace 2.1 mm long, 1.7 wide. First femur 2.5 mm, patella and tibia 2.9, metatarsus 1.7, tarsus 0.8. Second patella and tibia 2.4 mm, third 1.3, fourth 1.9.

Note. The male collected with the holotype has the embolus torn out.

Variation. Total length of females 5.6 to 5.8 mm, of males 3.8 to 4.0.

Diagnosis. The female is distinguished from *A. desierto* (Figs. 453, 454) by the shape of the posterior median plate of the epigynum (Fig. 450). The male is distinguished from *A. desierto* (Fig. 456) by the larger terminal apophysis (Fig. 452).

Paratypes. MEXICO *México:* Parque Nac. Zoquiapan, 3200 m, Aug. 1986, ♀ (W. Eberhard FN8-32, MCZ). *Distríto Federal:* 3.2 km W Río Frío, 3200 m, 24 July 1956 (W. Gertsch, V. Roth, AMNH).

Araneus desierto new species
Figures 453–456; Map 5

Holotype. Female holotype and male paratype from Desierto de los Leones, Distríto Federal, Mexico, 26 May 1946 (J. C., D. L. Pallister), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, dusky on sides of head and thorax. Sternum dark brown. Coxae light orange; legs orange with dusky rings. Dorsum of abdomen with a white transverse line from hump to hump, an indistinct folium posteriorly (Fig. 455). Venter dusky with a white line on each side, dusky white on sides of venter. Posterior median eyes 1.5 diameters of anterior medians, anterior lateral eyes same diameter as anterior medians, posterior laterals 0.8 diameter. Anterior median eyes 1.5 their diameter apart, 2.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen slightly longer than wide, with

humps (Fig. 455). Total length 3.8 mm. Carapace 1.8 mm long, 1.4 wide. First femur 1.9 mm, patella and tibia 2.2, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.9 mm, third 1.1, fourth 1.5.

Male. Carapace as in female. Dorsum of abdomen with paired white spots near anterior edge, no transverse white line, folium as in female, outlined by light line. Posterior median eyes 1.5 diameters of anterior medians, anterior lateral eyes 0.8 diameter, posterior laterals same diameter as anterior medians. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes their diameter apart, 1.7 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first. Abdomen as wide as long, with indistinct humps. Total length 3.3 mm. Carapace 1.5 mm long, 1.4 wide. First femur 2.0 mm, patella and tibia 2.5, metatarsus 1.3, tarsus 0.6. Second patella and tibia 2.2 mm, third 1.1, fourth 1.6.

Diagnosis. The female is distinguished from *A. dreisbachi* (Figs. 449, 450) by a longer scape (Fig. 453) and by a T-shaped median plate in posterior view (Fig. 454). The male is distinguished by a longer spine on the median apophysis (Fig. 456) than that of *A. dreisbachi* (Fig. 452) and by a differently shaped terminal apophysis.

Araneus leones new species
Figures 457–461; Map 5

Holotype. Female holotype, male paratype from Desierto de los Leones, Distríto Federal, Mexico, 5 Aug. 1946 (C. Goodnight, Bolivar, and Bonet), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace maculated orange, sides of head dusky. Sternum black. Coxae light orange; legs ringed black and dark orange. Dorsum of abdomen blackish brown with white folium outline and median white mark (Fig. 459); venter black with a white line on each side (Fig. 460). Posterior median eyes 1.3 diameters of anterior medians, lateral eyes same diameter as anterior medians. Anterior median eyes 1.2 diameters apart, 2 from laterals. Posterior median eyes 0.8 diameter apart, 2.5 from laterals. Abdomen slightly longer than wide, with humps (Fig. 459). Total length 4.5 mm. Carapace 1.9 mm long, 1.6 wide. First femur 2.1 mm, patella and tibia 2.7, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.3 mm, third 1.1, fourth 1.9.

Male. Coloration as in female, but without median white streak on abdomen. Posterior median eyes 1.2 diameters of anterior medians. Lateral eyes 0.9 diameter. Anterior medians 1.5 diameters apart, 1.5 from laterals. Posterior median eyes a little more than their diameter apart, 2.2 from laterals. First coxa without hook. Abdomen slightly wider than long. First and second tibiae of equal thickness. Total length 3.6 mm. Carapace 2.0 mm long, 1.6 wide. First femur 2.3 mm, patella and tibia 2.9, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.3 mm, third 1.3, fourth 1.9.

Variation. Total length of females 4.0 to 4.5 mm, of males 3.6 to 3.8. The markings on the abdomen are variable. The scape varies in length, but all have two twists. Five females had the scape coiled one way, three the other way, and one had the scape torn off.

Diagnosis. The female differs from females of most species by the coiled scape, and by the median posterior projection of the base of the epigynum (Figs. 457, 458). It differs from the female of *A. salto* (Figs. 462, 463) by the raised round edge on each side of the scape in ventral view (Fig. 457). The indistinct openings lie posteriorly on the circle formed by the edge (Fig. 457). The male differs by the large median apophysis, which is long and drawn out parallel to the cymbium, and is frayed at the other end (Fig. 461). The terminal apophysis, embolus and conductor are shaped differently than those of *A. popago* (Fig. 469).

Records. MEXICO *Distríto Federal:* Desierto de los Leones, June 1955, 5♀; 20 Nov. 1961, ♀; June 1965, 2♀ (N. L. H. Kraus, AMNH); 26 May 1946, 8♀, 5♂; 12 June 1946, ♀ (J. C., D. L. Pallister, AMNH).

Araneus salto new species
Figures 462–465; Map 5

Holotype. Female holotype and one female paratype from 16 km W of El Salto, Durango, Mexico (J. E. H. Martin), in CNC. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace dusky orange, darker dusky on sides; lightest in ocular quadrangle. Chelicerae dark orange with a dusky patch. Labium, endites dusky. Sternum dark dusky to black. Coxae light orange; legs light orange with narrow rings. Dorsum of abdomen has outline of folium brownish with symmetrical white areas anteriorly and posteriorly on sides (Fig. 464). Venter black between epigynum and spinnerets, a white band on each side (Fig. 465). Posterior median eyes 1.2 diameters of anterior medians, laterals 0.9 diameter. Anterior median eyes 1.2 diameters apart, 1.6 from laterals. Posterior median eyes 1.1 diameters apart, 2 from laterals. Abdomen as long as wide, with large humps (Fig. 464). Total length 4.3 mm. Carapace 2.0 mm long, 1.5 wide. First femur 2.0 mm, patella and tibia 2.5, metatarsus 1.6, tarsus 0.7. Second patella and tibia 2.1 mm, third 1.1, fourth 1.6.

Variation. The paratype illustrated (Fig. 464) has a much darker abdomen than the holotype, and its abdomen has setae that are lacking on the holotype.

Diagnosis. The epigynum of *A. salto* has a depression with the openings on each side of the scape in ventral view (Fig. 462); it lacks the round ridges of *A. leones* (Fig. 457). The median plate has two black patches some distance from the edge (Fig. 463).

Araneus popaco new species
Figures 466–469; Map 5

Holotype. Female holotype and male paratype from Volcán Popocatepetl, 3800 m, Est. México, Mexico, 14 Aug. 1954 (R. Dreisbach), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female. Carapace brown with light hairs; sternum dark brown. Coxae yellow; legs brown, ringed with black. Dorsum of abdomen brown with a white transverse band behind humps, and a posterior folium (Fig. 468). Venter with a pair of parallel longitudinal lines consisting of white pigment spots; spinnerets black. Posterior median eyes 1.3 diameters of anterior medians, lateral eyes same diameter as anterior medians. Anterior medians 1.5 diameters apart, 1.7 from laterals. Posterior medians their diameter apart, 2 from laterals. Abdomen as wide as long, with a pair of humps. Total length 5.6 mm. Carapace 2.0 mm long, 1.7 wide. First femur 2.1 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.3 mm, third 1.2, fourth 2.0.

Male from near Río Frío. Color as in female. Posterior median eyes 1.2 diameters of anterior medians, lateral eyes 0.8 diameter. Anterior median eyes 1.3 diameters apart, a little more than their diameter from laterals. Posterior median eyes their diameter apart, a little more than 2 from laterals. Endite with tooth. First coxa without hook. Second tibia slightly thicker than first. Abdomen subspherical, slightly longer than wide, with distinct humps (Fig. 468). Total length 4.2 mm. Carapace 2.0 mm long, 1.8 wide. First femur 2.5 mm, patella and tibia 3.1, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.5 mm, third 1.4, fourth 2.1.

Note. The male might be that of *A. ofrus.*

Diagnosis. Female differs from *A. leones* (Figs. 457, 458) by having the scape of the epigynum twisted only once (Fig. 466). The male differs from *A. leones* (Fig. 461) in the shape of the embolus, terminal

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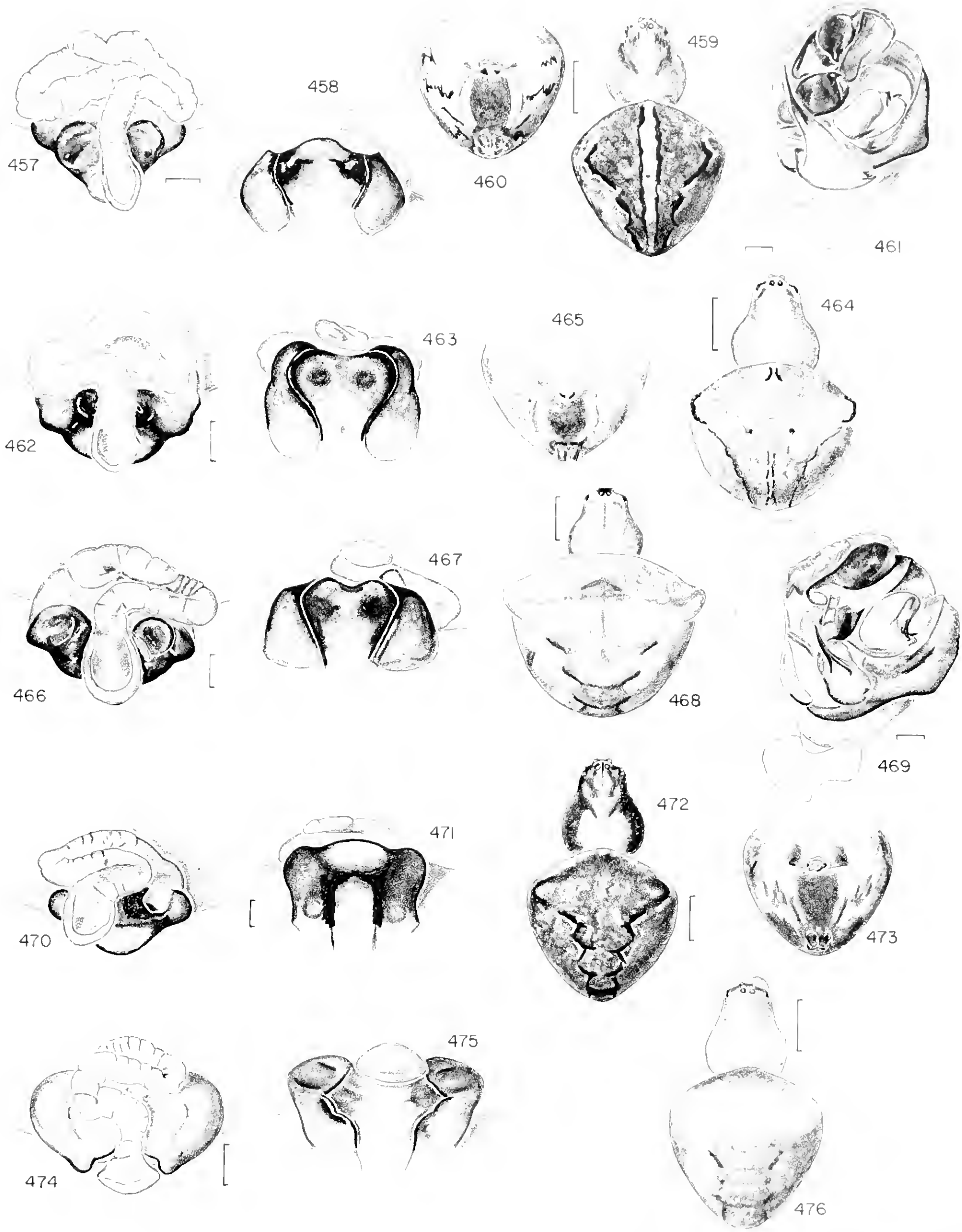
Figures 457–461. *Araneus leones* n. sp. 457–460. Female. 457. Epigynum, ventral. 458. Epigynum, posterior. 459. Dorsal. 460. Abdomen, ventral. 461. Male, left palpus.

Figures 462–465. *A. salto* n. sp., female. 462. Epigynum, ventral. 463. Epigynum, posterior. 464. Dorsal. 465. Abdomen, ventral.



Figures 466–469. *A. popaco* n. sp. 466–468. Female. 466. Epigynum, ventral. 467. Epigynum, posterior. 468. Dorsal. 469. Male palpus.

Figures 470–473. *A. quirapan* n. sp., female. 470. Epigynum, ventral. 471. Epigynum, posterior. 472. Dorsal. 473. Abdomen, ventral.

Figures 474–476. *A. nacional* n. sp., female. 474. Epigynum, ventral. 475. Epigynum, posterior. 476. Dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

[illegible] and tegulum (Fig. 469).

Paratypes. MEXICO *Distríto Federal:* W Paso de Cortez, 3400 m, 13 Aug. 1954, 2♀ (J. A. Chilcott, CNC); 3 km W Río Frío, 3200 m, 24 July 1956, 2♀, 2♂ (W. J. Gertsch, V. Roth, AMNH). *Michoacan:* Cerro de Tancitaro, 3200 m, July, Aug. 1941, 2♀ (H. Hoogstraal, MCZ).

Araneus quirapan new species
Figures 470–473; Map 5

Holotype. Female holotype, female paratype from Zoquiapan in the Parque Nacional Zoquiapan, Est. Mexico, 12 km SW of Rio Frio, 3200 m, ca 19°15'N, 98°21'W, Mexico, in forest dominated by *Abies religiosa* and *Pinus montezumae*, Aug. 1986 (W. Eberhard ENS-32), in MCZ. The specific name is an arbitary combination of letters.

Description. Female. Carapace orange near midline, with a median black line, black on sides, area between median eyes light, light yellowish on posterior slope of thorax (Fig. 472). Labium and endites black with light edges. Sternum black. Coxae yellow-white; legs contrastingly ringed black and yellow-white. Dorsum of abdomen dark brown to black, with outline of folium black (Fig. 472). Venter with a black rectangle between epigynum and spinnerets, light on sides of rectangle (Fig. 473). Eyes subequal. Anterior median eyes their diameter apart, 1.2 from laterals. Posterior medians 0.8 diameter apart, 2.5 from laterals. Abdomen wider than long, with large humps. Total length 5.5 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.1 mm, patella and tibia 2.7, metatarsus 1.6, tarsus 0.7. Second patella and tibia 2.4 mm, third 1.2, fourth 2.0.

Diagnosis. This species has a twisted scape (Fig. 470) with the openings on each side and median and lateral plates fused ventrally (Fig. 471).

Natural History. Eberhard (in letter) reports that the silk of the orb is yellow.

Araneus nacional new species
Figures 474–476; Map 5

[illegible] 60 km SW of Valle Nacional [illegible] line clearing through oak-pine forest along Hwy. 175 [near 17.5°N, 96.3°W], 2600 m, 25 June 1983 (W. Maddison), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace dark orange, head and clypeus darkest; sternum dusky dark orange. Coxae light orange; legs orange, indistinctly ringed. Dorsum of abdomen dark orange-gray, with outline of folium (Fig. 476); venter dusky with pair of white lines. Posterior median eyes and lateral eyes 1.3 diameters of anterior median eyes. Anterior median eyes 1.6 diameters apart, 2.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen as wide as long, with two humps (Fig. 476). Total length 4.7 mm. Carapace 2.1 mm long, 1.5 wide. First femur 2.0 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.6. Second patella and tibia 2.0 mm, third 1.1, fourth 1.6.

Diagnosis. This species is distinguished from other small species by the pair of tubercles on the posterior margin of the epigynum (Fig. 474) and the shape of the lateral plates in posterior view (Fig. 475).

Araneus mendoza new species
Figures 477–481; Map 5

Holotype. Male holotype, one male and one immature male paratypes from Ciudad Mendoza, Veracruz, Mexico, 24 Aug. 1964 (W. Ivie), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace dark orange, with white pigment under middle of thorax. Sternum dark, dusky on sides. Coxae light orange; legs dark orange with light rings. Dorsum of abdomen with dark folium on posterior half, sides blackish anteriorly (Fig. 480). Venter black between epigynum and spinnerets, with white line on each side. Posterior median eyes 1.5 diameters of anterior median eyes, lateral eyes same diameter as anterior medians. Anterior median eyes 1.5 diameters apart, 2.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen wider than long, with dorsal humps. Total length 3.5 mm. Carapace 1.5 mm

long, 1.3 wide. First femur 1.5 mm, patella and tibia 1.9, metatarsus 1.0, tarsus 0.6. Second patella and tibia 1.6 mm, third 0.9, fourth 1.3.

Male. Carapace darker than in female, dorsum of abdomen with contrasting pattern (Fig. 479). Posterior median eyes 1.2 diameters of anterior medians, anterior lateral eyes 0.7 diameter, posterior lateral eyes 0.9. Anterior median eyes 1.5 diameters apart, 2 from laterals. Posterior median eyes a little more than their diameter apart, 2.2 from laterals. Endite with tooth. First coxa without hook. Second tibia about as thick as first. Abdomen oval, with 2 humps. Total length 3.5 mm. Carapace 1.8 mm long, 1.6 wide. First femur 2.0 mm, patella and tibia 2.4, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.0 mm, third 1.0, fourth 1.4.

Variation. Total length of females 3.4 to 3.5 mm, of males 2.8 to 3.5. Of two females collected in Puebla, one is light colored (Fig. 480), the other dark.

Diagnosis. The female of *A. mendoza* differs from other species that have a scape with one twist by having the opening located posteriorly in a ventral fusion of median and lateral plates (Fig. 478). A sword-shaped embolus cap is stuck in each opening (Figs. 478). Males of *A. mendoza* are unlike all other *Araneus* species in having the embolus filament forming a large loop, and its basal plate round (Fig. 481).

Natural History. A male was collected in a cloud forest, a female in an oak forest at 2400 m, in Veracruz.

Distribution. Puebla and Veracruz States, Mexico (Map 5).

Paratypes. MEXICO *Puebla:* Tehuitaitlan, 1500 m [?], 9 July 1946, 2♀, ♂ (H. Wagner, AMNH). *Veracruz:* nr. Acultzingo, 2400 m, July 1953, ♀ (C. J. Goodnight, MCZ, ex AMNH); 17.6 km S Misantla, 24 July 1984, ♂ (J. B. Woolley, MCZ).

Araneus puebla new species
Figures 482–486; Map 5

Holotype. Female holotype and male paratype from Huauchinango, Puebla, Mexico, 7 Oct. 1947 (H. M. Wagner), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange, sides of thorax dusky. Sternum dusky brown. Coxae light orange; legs orange, third and fourth legs with lighter orange rings. Dorsum of abdomen with white anterior triangle and posterior dark folium (Fig. 484). Venter black between epigynum and spinnerets with white mark on each side (Fig. 485). Eyes subequal. Anterior median eyes 1.2 diameters apart, 1.2 from laterals. Posterior medians their diameter apart, 2.2 from laterals. Abdomen with shoulder humps (Fig. 484). Total length 3.2 mm. Carapace 1.6 mm long, 1.3 wide. First femur 1.6 mm, patella and tibia 1.9, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.6 mm, third 0.9, fourth 1.3.

Male. Color as in female. Posterior median eyes same diameter as anterior medians, anterior laterals 0.9 diameter, posterior laterals 0.7. Anterior medians a little more than their diameter apart, a little less than their diameter from laterals. Posterior medians 0.7 diameter apart, 1.5 from laterals. Endite with tooth. Small tubercle distally on posterior face of fourth coxae. Abdomen oval, longer than wide, widest anteriorly, with indistinct humps. Total length 3.1 mm. Carapace 1.4 mm long, 1.3 wide. First femur 2.1 mm, patella and tibia 2.3, metatarsus 1.5. Second patella and tibia 1.9 mm, third 0.9, fourth 1.4.

Diagnosis. The female has a twisted scape (Fig. 482) but differs from others by having the openings posteriorly in a round depression (Fig. 483). The male is distinct in having the filamentous part of the embolus about equal in length to the diameter of its base (Fig. 486).

Araneus guerrerensis Chamberlin and Ivie
Figures 487–493; Map 5

Araneus guerrerensis Chamberlin and Ivie, 1936: 45, pl. 13, figs. 117–118, ♀. Female holotype from Chilapa, Guerrero, Mexico, legs broken off, in ZMB, no. 22022, examined. Roewer, 1942: 844. Bonnet, 1955: 512.

Araneus chiricahua Levi, 1973: 496, figs. 44–54, ♀, ♂.

[illegible] Southwestern Research Station, 8 km W of Portal, Arizona, in MCZ. Brignoli, [illegible]: 261. NEW SYNONYMY.

Description. Female. Carapace orange to dusky orange, lightest in middle of thorax, sides darkest. Sternum brown with anterior small orange spot. Coxae light dusky orange, legs dusky orange. Dorsum of abdomen white and dusky with indistinct folium posteriorly containing transverse bars. Anterior with white chevron (Figs. 491, 492). Venter between epigynum and spinnerets dusky, sides with dusky white pigment spots. Posterior median eyes 1.5 diameters of anterior medians, lateral eyes same diameter as anterior medians. Anterior medians 2 times their diameter apart, 3 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen spherical, with large humps. Total length 4.3 mm. Carapace 1.8 mm long, 1.4 wide. First femur 1.9 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.9 mm, third 1.1, fourth 1.5.

Male from Morelos. Color as in female. Posterior median eyes 1.4 diameters of anterior medians, anterior lateral eyes 0.8 diameter, posterior laterals 0.9. Anterior medians 1.5 their diameter apart, 2.5 from laterals. Posterior median eyes their diameter apart, 2 from laterals. First coxa without hook. Second tibia slightly thicker than first. Total length 3.4 mm. Carapace 1.7 mm long, 1.4 wide. First femur 1.7 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.2, fourth 1.4.

Variation. Total length of females 3.1 to 4.3 mm, of males 2.8 to 3.6.

Diagnosis. The epigynum has a twisted scape; the openings, unlike those of related species, are in a slit on each side (Figs. 487, 488). The posterior plates are fused ventrally (Figs. 489, 490). The male, unlike similar species, has the tip of the embolus coiled (Fig. 493).

Distribution. Southeastern Arizona to [illegible] Mexico (Map 5).

Records. MEXICO *Durango:* [illegible] Aug. 1947 [illegible] W. J. Gertsch, AMNH). *Distríto Federal:* El Xitle, 12 Oct. 1942, 2♀ (C. Tellez, AMNH); W Río Frío, 22 Aug. 1964, 5♀, 4♂ (J., W. Ivie, AMNH). *México:* Amecameca, 29 Sept. 1957, 2♀, ♂ (R. Dreisbach, MCZ).

Araneus anguinifer (F. P.-Cambridge)
Figures 494–496; Map 5

Aranea anguinifera F. P.-Cambridge, 1904: 514, pl. 49, fig. 14, ♀. Female holotype from Omilteme, 16 km WSW of Chilpancingo, 2600 m, Guerrero, Mexico, in BMNH, examined. Roewer, 1942: 837.
Araneus anguinifer:–Bonnet, 1955: 432.

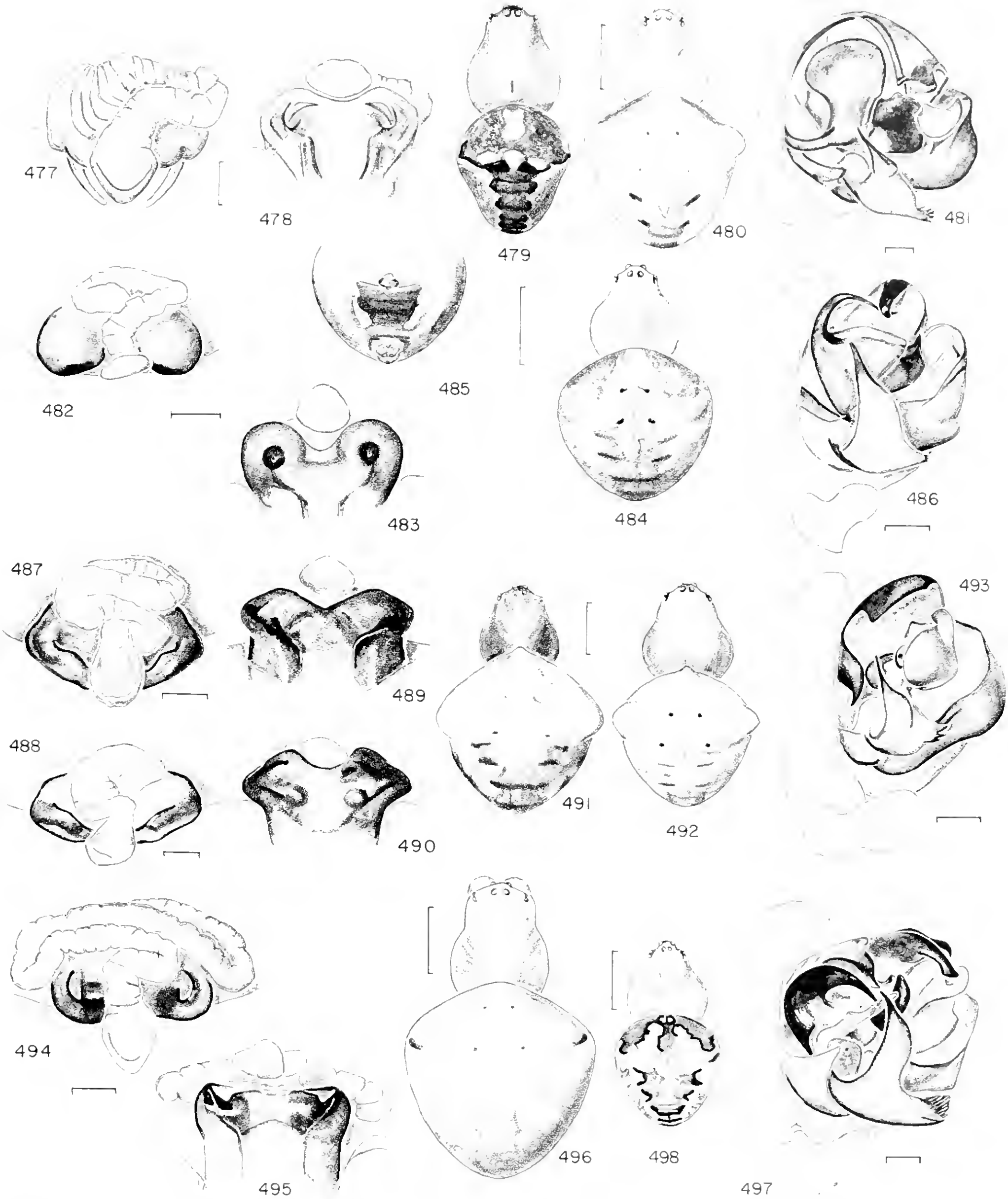
Description. Female. Carapace yellow, sides of thorax darker. Coxae, legs yellow. Dorsum of abdomen with a dark spot on each hump and a small light mark behind, a posterior dorsal dark band (Fig. 496), venter dark gray. Posterior median eyes 2 diameters of anterior medians, laterals 1.3 diameters. Anterior medians 2 diameters apart, 3.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen almost as wide as long, with two humps (Fig. 496). Total length 4.5 mm. Carapace 2.4 mm long, 1.6 wide. First femur 2.3 mm, patella and tibia 3.0, metatarsus 2.4, tarsus 0.9. Second patella and tibia 2.6 mm, third 1.3, fourth 2.0.

Diagnosis. The scape of the epigynum of this species is the longest of all *Araneus* species, and is bent over four times (Fig. 494). There is a notch on each side of the base in ventral view (Fig. 494).

Araneus huixtla new species
Figures 497, 498; Map 5

Holotype. Male holotype from 54 km N of Huixtla, 1800 m, Chiapas, Mexico, 26 Feb. 1966 (G. Ball, D. R. Whitehead), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace dusky yellowish with white pigment patch in middle. Chelicerae yellowish with dusky patch. Labium, endites dusky. Sternum yellowish, dusky on sides with some white pigment anteriorly. Coxae light orange; legs yellowish with dark dusky rings most distinct on third and fourth legs. Dorsum of abdomen with contrasting folium pattern (Fig. 498); venter black anterior of spin-



Figures 477–481. *Araneus mendoza* n. sp. 457–480. Female. 477. Epigynym, ventral. 478. Epigynum, posterior. 479, 480. Dorsal. 479 (holotype). 480 (paratype). 481. Male, left palpus.

Figures 482–486. *A. puebla* n. sp. 482–485. Female. 482. Epigynum, ventral. 483. Epigynum, posterior. 484. Dorsal. 485. Abdomen, ventral. 486. Male palpus.

Figures 487–493. *A. guerrerensis* Chamberlin and Ivie. 487–492. Female. 487, 488. Epigynum, ventral. 489, 490. Epigynum, posterior. 491, 492. Dorsal. 487, 489, 491 (holotype). 488, 490, 492 (Morelos, Mexico). 493. Male palpus.

Figures 494–496. *A. anguinifer* (F. P.-Cambridge), female. 494. Epigynum, ventral. 495. Epigynum, posterior. 496. Dorsal.

Figures 497, 498. *A. huixtla* n. sp., male. 497. Palpus. 498. Dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

nerets with a white bracket on each side. Posterior median eyes 1.2 diameters of anterior medians, laterals same diameter as anterior medians. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes slightly less than 1 diameter apart, 2.7 from laterals. Endite with tooth. First coxa without hook. Second tibia same thickness as first. Abdomen oval, with humps (Fig. 498). Total length 3.4 mm. Carapace 1.8 mm long, 1.5 wide. First femur 2.5 mm, patella and tibia 2.9, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.1 mm, third 1.1, fourth 1.6.

Diagnosis. This male differs from others by having a heavy, spine-shaped, curved embolus (Fig. 497).

Araneus ocaxa new species
Figures 499–502; Map 5

Holotype. Female holotype, two male paratypes from 60 km SW of Valle Nacional, Oaxaca, Mexico, on Hwy. 175, near 17.5°N, 96.5°W, 2600 m, power line clearing through oak-pine forest, 25 June 1983 (W. Maddison), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female. Carapace orange. Sternum brown. Coxae and legs orange. Dorsum of abdomen beige with brown folium (Fig. 501); venter with median dark band and lighter sides. Posterior median eyes 1.5 diameters of anterior median eyes, lateral eyes same diameter as anterior median eyes. Anterior median eyes 3 diameters apart, 4 from laterals. Posterior median eyes 1.5 diameters apart, a little over 3 from laterals. Abdomen as wide as long, with two humps (Fig. 501). Total length 3.9 mm. Carapace 1.9 mm long, 1.4 wide. First femur 1.7 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.9 mm, third 1.1, fourth 1.6.

Male. Darker than female, with ringed legs. Eyes subequal. Anterior median eyes 1.5 diameters apart, 2 from laterals. Posterior median eyes a little more than their diameter apart, 2.2 from laterals. Endite with tooth. First coxa without hook. First and second tibiae of equal thickness, first with some macrosetae. Total length 3.6 mm. Carapace 1.8 mm long, 1.6 wide. First femur 2.1 mm, patella and tibia 2.4, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.1 mm, third 1.0, fourth 1.5.

Diagnosis. The female differs from *A. mendoza* (Figs. 477, 478) by having the openings of the epigynum in V-shaped depressions on the venter (Fig. 499), the male by having a shorter embolus (Fig. 481).

Araneus baul new species
Figures 503–506; Map 5

Holotype. Female from 21 km W of Rizo de Oro, along ridge SE of Cerro Baúl, border Oaxaca, Chiapas, Mexico, cloud forest, 1615 m, 6–8 Sept. 1972 (C. Mullinex, D. E. Breedlove), in CAS. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange, a diagonal dusky streak on each side. Chelicerae orange. Labium dark dusky. Endites dusky. Sternum black on each side, orange in middle. Coxae orange; legs light orange. Dorsum of abdomen dusky white with a transverse white band (Fig. 505); venter with a black mark between epigynum and spinnerets, otherwise white (Fig. 506). Posterior median eyes 1.3 diameters of anterior medians, laterals same diameter as anterior medians. Anterior median eyes slightly more than 1 diameter apart, the same from laterals. Posterior median eyes 0.7 their diameter apart, 1.5 from laterals. Abdomen as wide as long with lateral and anterior median humps (Fig. 505). Total length 3.6 mm. Carapace 1.6

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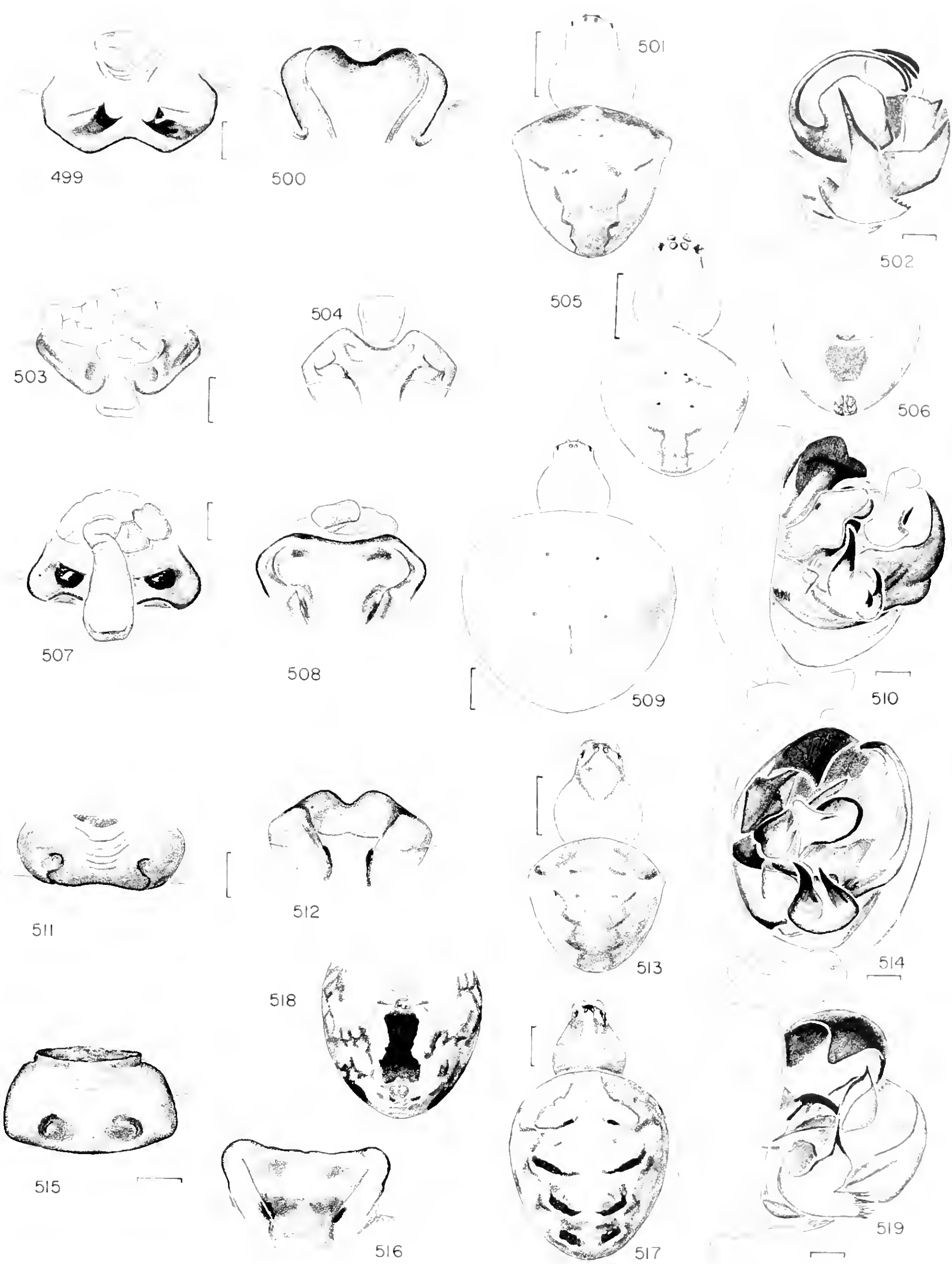
Figures 499–502. *Araneus ocaxa* n. sp. 499–501. Female. 499. Epigynum ventral. 500. Epigynum, posterior. 501. Dorsal. 502. Male, left palpus.

Figures 503–506. *Araneus baul* n. sp., female. 503. Epigynum, ventral. 504. Epigynum, posterior. 505. Dorsal. 506. Abdomen, ventral.

Figures 507–509. *A.* [illegible] (Banks). 507–509. Female. 507. Epigynum, ventral. 508. Epigynum, posterior. 509. Dorsal.



Figures 511–514. *A. tenancingo* n. sp. 511–513. Female. 511. Epigynum, ventral. 512. Epigynum, posterior. 513. Dorsal. 514. Male palpus.

Figures 515–519. *A. tellezi* n. sp. 515–518. Female. 515. Epigynum, ventral. 516. Epigynum, posterior. 517. Dorsal. 518. Abdomen, ventral. 519. Male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

mm long, 1.1 wide. First femur 1.8 mm, patella and tibia 2.1, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.8 mm, third 1.0, fourth 1.5.

Diagnosis. The female differs from that of *A. nacional* (Figs. 474, 475) by having the sides of the base of the epigynum diagonal on each side, and from *A. mendoza* (Figs. 477, 478) by having a longer, narrower scape (Fig. 503).

Araneus arizonensis (Banks)
Figures 507–510; Map 5

Epeira arizonensis Banks, 1900: 100. Female holotype from Arizona in MCZ, examined. Banks, 1901: 585, pl. 22, fig. 5, ♂.
Neosconella arizonensis:—Archer, 1951a: 38.
Conaranea gertschi:—Archer, 1951b: 7, figs. 17, 30, ♀. Misidentification.
Araneus arizonensis:—Levi, 1973: 497, figs 60–71, ♀, ♂.

Description. Female from Chihuahua, Mexico. Carapace light orange; sternum orange. Legs light orange. Dorsum of abdomen orange-white; venter with a white rectangle between epigynum and spinnerets. Eyes subequal. Anterior median eyes 1.2 their diameter apart, 1.5 from laterals. Posterior median eyes their diameter apart, a little less than 3 from laterals. Abdomen wider than long, with humps (Fig. 509). Total length 6.9 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.5 mm, patella and tibia 3.1, metatarsus 1.9, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.7, fourth 2.3.

Male from Coahuila. Carapace dusky orange to orange-brown. Coxae orange; legs brown. Dorsum of abdomen with a speckled folium and a dark outline bordered by white; venter with a white square. Secondary eyes 0.8 diameter of anterior medians. Anterior median eyes their diameter apart, 1.5 from laterals. Posterior median eyes a little less than their diameter apart, 3 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first, first with more macrosetae. Abdomen widest anteriorly. Total length 4.3 mm. Carapace 2.1 mm long, 1.8 wide. First femur 2.5 mm, patella and tibia 3.1, metatarsus 2.1, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.6, fourth 2.2.

Diagnosis. The epigynum of the female differs from others by showing the seminal receptacles in a dark spot on each side of the scape (Fig. 507). The male palpus is distinguished by having three, almost parallel, large spines on the median apophysis (Fig. 510).

Distribution. Southern Colorado, New Mexico, Arizona to northern Mexico (Map 5).

Additional Records. MEXICO *Coahuila:* Guadalupe, 24 May 1952, ♂ (M. Cazier, W. J. Gertsch, AMNH). *Chihuahua:* 32 km W Matachic, 7 July 1947, ♀ (W. J. Gertsch. AMNH).

Araneus tenancingo new species
Figures 511–514; Map 5

Holotype. Female holotype and male paratype from Tenaningo [Tenancingo], Est. México, Mexico, 2050 m, 27 Sept.–7 Oct. 1946 (H. Wagner), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, head dusky, with dusky line from posterior median eyes to sides of head, another from sides of head to middle of thorax. Sternum black; coxae light orange. Legs orange with dusky rings. Dorsum of abdomen brownish, lighter behind, with paired diagonal marks (Fig. 513). Venter black, bordered by white bracket on each side. Posterior median eyes 1.3 diameters of anterior medians, anterior lateral eyes 0.8 diameter, posterior laterals same diameter as anterior medians. Anterior medians 1.5 their diameter apart, 1.5 from laterals. Posterior medians 1.2 their diameter apart, a little less than 2 from laterals. Abdomen slightly longer than wide, with pair of humps. Total length 4.0 mm. Carapace 1.8 mm long, 1.4 wide. First femur 2.2 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 0.8. Second patella and tibia 2.1 mm, third 1.0, fourth 1.7.

Male. Carapace orange, sides dark, dusky, with indistinct dark line from pos-

terior median eye to side. Sternum blackish, underlain by white spot anteriorly. Coxae light orange; legs orange, with indistinct dark rings. Dorsum of abdomen as in female; venter dusky with pair of white lines. Posterior median eyes 0.8 diameter of anterior medians, anterior lateral eyes 0.6 diameter, posterior laterals 0.7. Anterior medians their diameter apart, their diameter from laterals. Posterior medians 1.2 their diameter apart, 2.2 from laterals. Conductor without tooth at base. Palpus with two setae on tibia (one shown in Fig. 514); endite with tooth. First coxa without hook. First tibia thicker and with more macrosetae than second. Abdomen slightly longer than wide, with pointed humps. Total length 3.5 mm. Carapace 1.8 mm long, 1.6 wide. First femur 2.3 mm, patella and tibia 2.6, metatarsus 1.7, tarsus 0.8. Second patella and tibia 2.3 mm, third 1.2, fourth 1.6.

Note. It is uncertain whether this male belongs with the female. The coloration is as in female, but the anterior median eyes are larger than others.

Diagnosis. The female differs from others by having the genital openings in a depression on the ventral side, in the end of the seam between the median and lateral plates (Figs. 511, 512). In posterior view the median plate has a ventral notch (Fig. 512). The scape is torn off the epigynum (Fig. 511). The male has a distinctive median apophysis with two large spines, almost parallel, directed apically (Fig. 514).

Araneus tellezi new species
Figures 515–519; Map 5

Holotype. Female holotype with two female and two male paratypes from El Xitle, Distríto Federal, Mexico, 12 Oct. 1942 (C. Tellez), in AMNH. The species is named after the collector.

Description. Female. Carapace orange-yellow, sides of head dusky, white pigment spot on thorax. Sternum dark brown; coxae orange-yellow. Legs orange-yellow with narrow, dark brown, distinct rings. Dorsum of abdomen with paired black bars forming a folium outlined by white, and a white chevron anterior to folium (Fig. 517). Sides marbled with black. Venter has a median black rectangle with a white patch on each side (Fig. 518). Posterior median eyes 1.5 diameters of anterior medians, lateral eyes same diameter as anterior medians. Anterior medians 1.5 diameters apart, 1.5 from laterals. Posterior medians a little more than their diameter apart, 2.2 from laterals. Abdomen oval, with slight humps, narrower posteriorly (Fig. 517). Total length 6.4 mm. Carapace 2.0 mm long, 1.6 wide. First femur 2.3 mm, patella and tibia 2.7, metatarsus 1.6, tarsus 0.7. Second patella and tibia 2.3 mm, third 1.3, fourth 1.9.

Male. Color as in female. Posterior median eyes 1.3 diameters of anterior medians, lateral eyes same diameter as anterior medians. Anterior medians 1.3 diameters apart, 1.3 from laterals. Posterior medians their diameter apart, 2 from laterals. Endite with tooth. First coxa without hook. Second tibia thinner than first, first with macrosetae. Total length 3.4 mm. Carapace 1.8 mm long, 1.5 wide. First femur 2.1 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 1.1. Second patella and tibia 2.0 mm, third 1.1, fourth 1.6.

Diagnosis. The female has the scape torn. Females of *A. tellezi* have, unlike those of related species, the oval abdomen longer than wide (Fig. 517), the openings in round depressions on the ventral surface of the base of the epigynum (Fig. 515), and the median posterior plate triangular (Fig. 516). The male is distinguished from males of *A. guerrerensis* (Fig. 493) by the shape of the coiled embolus and the domed terminal apophysis (Fig. 519).

Dubiepeira new genus

Type species. *Metepeira dubitata* Soares and Camargo, 1948. The name *Dubiepeira* refers to doubtful generic placement of several species here assigned to it. The name is of feminine gender.

Diagnosis. The female epigynum is

tated and not only the posterior margin and the posterior aspect sclerotized; the area from which the scape originates is soft (Figs. 520, 521). This is a presumed apomorphy.

The male's palpus is distinct; the median apophysis has a spur on its side extending laterally and distally, a presumed apomorphic character (Figs. 524–526, 535).

Note. Unfortunately, males are known for only two species, and the single male of *D. amacayacu* (Fig. 535) is shrivelled; it may once have been dry.

Description. The females (Fig. 522) are much like those of *Araneus*, but are glabrous, and the abdomen is oval to spherical and never has dorsal humps (Figs. 522, 529). Most importantly, the epigynum is relatively small.

The males are much smaller than the females. The palpal patella has two macrosetae, the endite lacks a tooth and the first coxa has no hook. The second tibia is not modified; it is as thick as the first. (In males of most *Araneus* species the size of *Dubiepeira* males, the endite has a tooth, the first coxa has a hook, and the second tibia is modified.)

Relationship. The genus is close to *Araneus*, and with *Araneus* it shares general appearance, spherical abdomen, wrinkled scape of the epigynum, and the three plates of the epigynum in posterior view. Also in both genera, the conductor of the male palpus sits on the rim of the tegulum (Figs. 525, 526) and there is a large terminal apophysis. *Dubiepeira* is distinct in the small size and light sclerotization of the epigynum and the unusual shape of the median apophysis and palpal tibia (Figs. 524–526).

Natural History. Dubiepeira dubitata females are found in humid locations, the female in a curled leaf retreat to the side of a large orb.

Distribution. All species here assigned to the genus are found in the Amazon drainage, and the range of *D. dubitata* extends to southern Brazil (Map 6).

KEY TO SPECIES OF *DUBIEPEIRA*

1	Males	2
–	Females	3
2(1)	Sickle-shaped terminal apophysis and bulky embolus behind the conductor (Fig. 535)	*amacayacu*
–	Terminal apophysis bow-shaped and embolus a slender thread (Figs. 524, 526)	*dubitata*
3(2).	In posterior view, median plate of epigynum with transverse bar (Fig. 521)	*dubitata*
–	Median plate without transverse bar (Figs. 528, 532, 537, 541)	4
4(3).	Ventral edge of median plate with pair of concave indentations (Fig. 528)	*neptunina*
–	Median plate otherwise	5
5(4).	Median plate with pair of lateral lobes (Fig. 541)	*amablemaria*
–	Median plate otherwise (Figs. 532, 537)	6
6(5).	Median plate with ventral convex edge (Fig. 532)	*amacayacu*
–	Median plate ventrally fused with lateral plates (Fig. 537)	*lamolina*

Dubiepeira dubitata (Soares and Camargo) new combination

Plate 2; Figures 520–526; Map 6

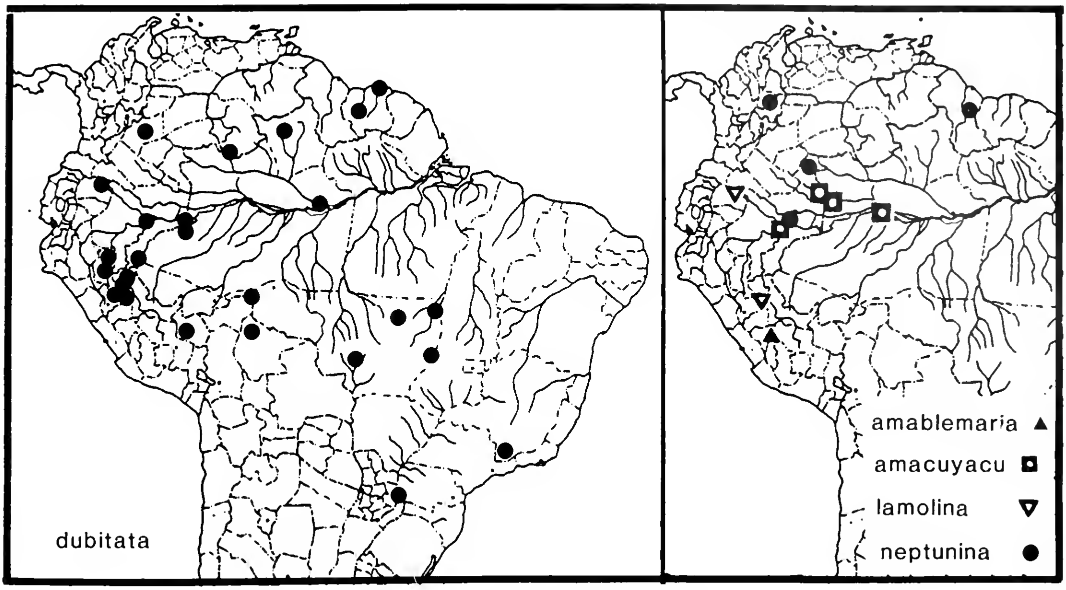
Metepeira dubitata Soares and Camargo, 1948: 375, figs. 30, 31, ♀, Female holotype and one paratype from Chavantina, Mato Grosso, Brazil, in MZSP nos. 1302, 1303, examined. Brignoli, 1983: 275.

?*Neosconella compsa* Soares and Camargo, 1948: 376, fig. 32, ♂, Male with both palpi lost, from Aragarças, Rio Araguaia confluence with Rio das Garças, Goiás, Brazil, in MZSP no. 1307, examined.

?*Araneus compsus*:—Brignoli, 1983: 262.

Note. The coloration suggests that the male *compsa* belongs with the female of *D. dubitata*. The palpus of the male illustrated by Soares and Camargo appears mounted and squashed on a slide. The second tibia of the *N. compsa* holotype is slightly thicker than the first.

Description. Female from Colombia. Carapace orange with black marks (Fig. 522). Sternum black. Coxae orange with black marks. Legs orange with contrasting black rings. Dorsum of abdomen white (Fig. 522), sides black, venter with a white spot on a light band on each side (Fig. 523). Secondary eyes 0.6 diameter of anterior



Map 6. Distribution of *Dubiepeira* species.

medians. Anterior median eyes 0.8 diameter apart, 2 from laterals. Posterior median eyes 0.6 diameter apart, 4 from laterals. Abdomen spherical (Fig. 522). Total length 12.7 mm. Carapace 5.9 mm long, 4.7 wide. First femur 6.0 mm, patella and tibia 7.5, metatarsus 5.8, tarsus 2.1. Second patella and tibia 6.7 mm, third 3.9, fourth 6.0.

Male from Colombia. Carapace yellow-white with median brown line, sides of thorax brown. Chelicerae, labium, endites, sternum black. Coxae yellow-white. Legs contrastingly ringed black and yellow-white. Dorsum of abdomen white, venter dusky to black. Thoracic depression round with plus-shaped mark. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.6 diameter apart, 0.6 from laterals. Posterior median eyes 0.6 diameter apart, 2 from laterals. Endite without tooth. First coxa without hook. Second tibia as thick as first. Abdomen oval, widest anteriorly. Total length 4.5 mm. Carapace 2.7 mm long, 2.0 wide. First femur 2.9 mm, patella and tibia 3.7, metatarsus 2.9, tarsus 1.2. Second patella and tibia 3.1 mm, third 1.7, fourth 2.5.

Variation. A photograph of a female shows the carapace to be brown, the legs white with black rings, and the abdomen bright green (Plate 2). The holotype of *dubitata* has an orange sternum, and the legs are not ringed. Total length of females 11.4 to 14.4 mm, of males 3.6 to 6.5. Some females have the transverse bar of the posterior plate bent, chevron-like.

Diagnosis. The female differs from other *Dubiepeira* species by having a transverse sclerotized bar on the median plate of the epigynum in posterior view (Fig. 521). The male differs from that of *D. amacayacu* (Fig. 535) by having a slender curved embolus (Figs. 524–526).

Natural History. Females have been collected from a bottom land swamp-forest, Madre de Dios Dpto., Peru; "fell into dugout canoe from overhanging vegetation in Venezuela"; on a moist slope facing Iguazu Falls in Paraná, Brazil. The female builds a curled-leaf retreat.

Distribution. Amazon drainage to Parana State, Brazil (Map 6).

Records. VENEZUELA *Amazonas:* Upper Río Baria, 100 m (AMNH). SURINAM Voltzberg-Raleighvallen Reserve (MCZ); Republiek (AMNH). COLOMBIA *Meta:* Puerto Lleras, Lomalinda (MCZ). ECUADOR *Napo:* Aguas Negras, Tarapuy (MECN); Reserva Faunistica Cuyabeno, Laguna Grande (MCZ); Río Tarapuy, at junction with Tarapoa road (MCZ); Pompeya, Napo River (MCZ). PERU *Loreto:* Río Momón near Iquitos (CAS); Río Bambo, Alto Tapiche (AMNH). *San Martín:* Bella Vista (AMNH); Hera, 20 km SE Moyobamba (AMNH). *Ucayali:* Pucallpa (CAS). *Huánuco:* Tingo María (AMNH); Monsón Valley, Tingo María (CAS); Parque Nac. A. von Humboldt (MHNSM); Jantas, La Molina (MHNSP). *Madre de Dios:* Parque Nac. Manu (MHNSM); N. R. Manu (USNM). BOLIVIA *Beni:* Chacobo Indian Village, Río Benicito (AMNH). BRAZIL *Roraima:* Ilha de Maracá, Amazonia (INPA); Ouro Prêto do Oeste, Faz. Nova Umás (MNRJ); Ilha de Maracá, Alto Alegre (INPA). *Amazonas:* Igarapé Belém nr. confluence with Rio Solimoes (INPA); Manaus (MEG); Benjamin Constant (MNRJ). *Rondônia:* Abunã (MCZ). *Mato Grosso:* Barra do Tapirapé (AMNH); Xingu, Jacaré (AMNH); Barra dos Bugres (MNRJ); Chavantina (MZSP). *Minas Gerais:* Lavras (MCZ). *Paraná:* Iguaçu Falls (MCZ).

Dubiepeira neptunina (Mello-Leitão) new combination

Figures 527–530; Map 6

Neosconella neptunina Mello-Leitão, 1948: 170, figs. 12–14. ♀. Female holotype from Yawakuri River, Guiana, in BMNH, examined.
Araneus neptuninus:—Brignoli, 1983: 263.

Description. Female holotype. Carapace orange. Chelicerae, labium, endites, sternum orange. Coxae, legs orange with a black ring around distal end of each tibia. Dorsum of abdomen white with some black marks (Fig. 529); sides with black patches; venter with black square between epigynum and spinnerets (Fig. 530). Secondary eyes 0.7 diameter of anterior medians. Anterior median eyes 0.5 diameter apart, 1.3 from laterals. Posterior median eyes 0.4 diameter apart, 2.5 from laterals. Abdomen spherical. Total length 9.4 mm. Carapace 4.0 mm long, 2.9 wide. First femur 3.4 mm, patella and tibia 4.5, metatarsus 3.1, tarsus 1.3. Second patella and tibia 3.8 mm, third 2.5, fourth 3.6.

Diagnosis. In posterior view of the epigynum the median plate has a pair of concave margins ventrally (Fig. 528), lacking the transverse bar of *D. dubitata* (Fig. 521).

Records. COLOMBIA *Santander:* Río Suárez, 800–1000 m, 11–17 Aug. 1946, ♀ (AMNH). *Vaupés:* Río Vaupés, Apr. 1906, ♀ (AMNH). PERU *Loreto:* 80 km NE Iquitos, 16–20 July 1989, 2♀ (G. B. Edwards, FSCA).

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Figures 520–526. *Dubiepeira dubitata* (Soares and Camargo). 520–523. Female. 520. Epigynum, ventral. 521. Epigynum, posterior. 522. Dorsal. 523. Abdomen, ventral. 524–526. Male, left palpus. 524. Mesal. 525. Lateral. 526. Pulled apart.

Figures 527–530. *D. neptunina* (Mello-Leitão), female. 527. Epigynum, ventral. 528. Epigynum, posterior. 529. Dorsal. 530. Abdomen, ventral.

Figures 531–535. *D. amacayacu* n. sp. 531–534. Female. 531. Epigynum, ventral. 532. Epigynum posterior. 533. Dorsal. 534. Abdomen, ventral. 535. Male palpus (damaged).

Figures 536–539. *D. lamolina* n. sp., female. 536. Epigynum, ventral. 537. Epigynum, posterior. 538. Dorsal. 539. Abdomen, ventral.

Figures 540–542. *D. amablemaria* n. sp., female. 540. Epigynum, ventral. 541. Epigynum, posterior. 542. Dorsal.

Abbreviations. C, conductor; DH, distal hematodocha; E, embolus; H, hematodocha; M, median apophysis; R, radix; T, tegulum; TA, terminal apophysis.

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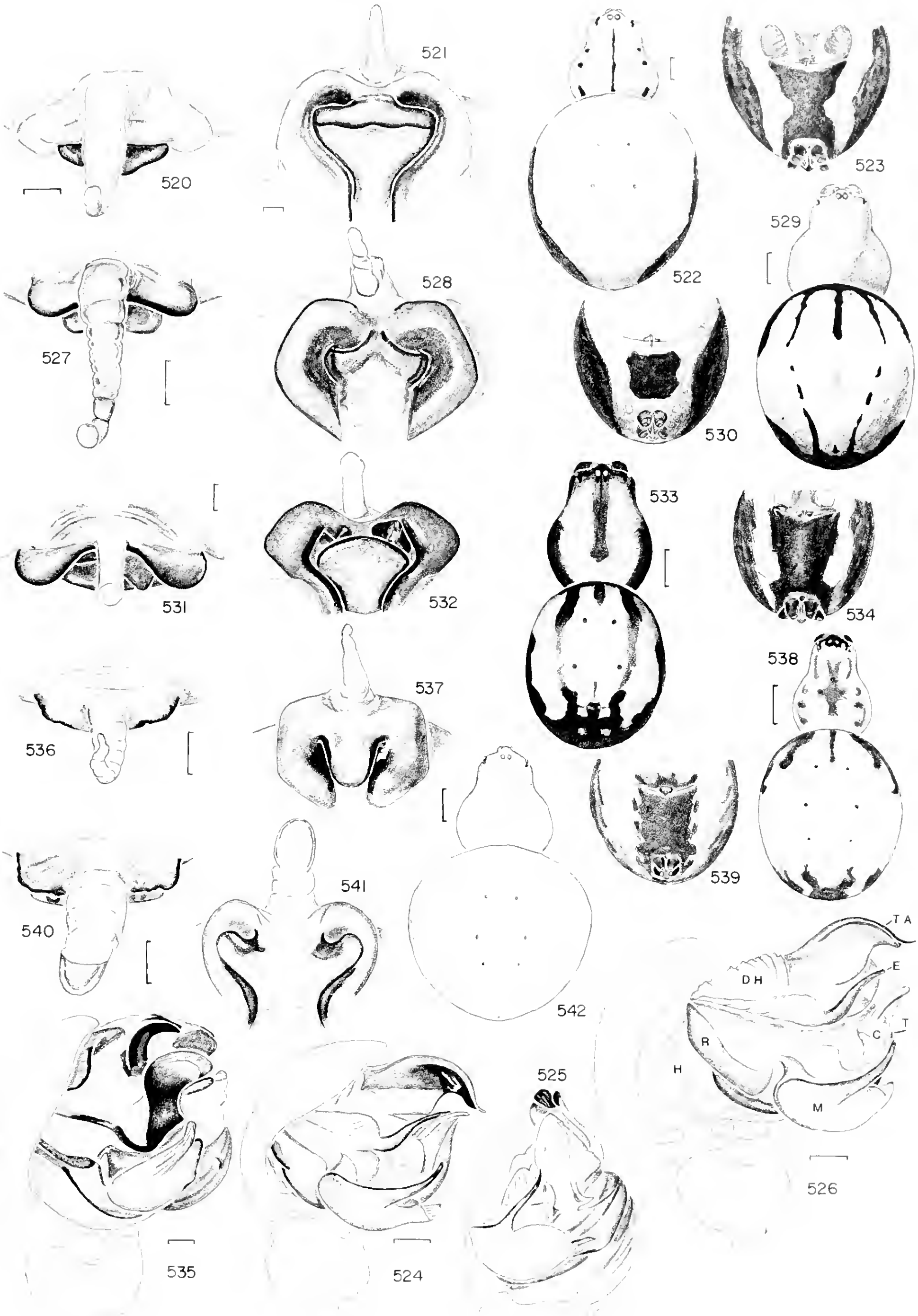
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Dubiepeira amacayacu new species
Figures 531–535; Map 6

Holotype. Female holotype from Amacayacú, Parque Nacional ca. 48 km NW of Leticia, 90–100 m, 70°16′W, 3°48′S, Dpto. Amazonas, Colombia, 3 Oct. 1985, on ground-growing fungus in primary forest (H. Sturm), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace light orange, sides of thorax with black band, eye region black and a median black band on head (Fig. 533). Chelicerae, labium, endites, and sternum black. Coxae light orange; legs light orange with wide black rings. Dorsum of abdomen white with contrasting symmetrical black marks (Fig. 533); venter black with light marks on each side (Fig. 534). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 0.7 diameter apart, 1 from laterals. Posterior median eyes 0.4 their diameter apart, 2 from laterals. Abdomen oval (Fig. 533). Total length 8.6 mm. Carapace 3.5 mm long, 2.8 wide. First femur 3.5 mm, patella and tibia 4.0, metatarsus 2.9, tarsus 1.2. Second patella and tibia 3.7 mm, third 2.1, fourth 3.4.

Male. Coloration slightly darker than in female; dorsum of abdomen with two black bands. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1 diameter apart, 1 from laterals. Posterior median eyes 0.3 diameter apart, 2 from laterals. Second tibia as thick as first. Abdomen oval. Total length 5.2 mm. Carapace 2.9 mm long, 2.3 wide. First femur 3.3 mm, patella and tibia 3.9, metatarsus 3.1, tarsus 1.3. Second patella and tibia 3.2 mm, third 1.9, fourth 2.9.

Note. The male was matched with the female on the basis of the coloration and markings on the abdomen, especially the venter.

Diagnosis. The ventral, convex margin of the median plate of the epigynum (Fig. 532) and the large bulky embolus of the male palpus (Fig. 535) separate this species from other *Dubiepeira*.

Paratypes. COLOMBIA *Amazonas:* Leticia, 21 June 1965, 7♀, 2 imm. (P. R. Craig, J. Robb, DU). PERU *Loreto:* 40 km NE Iquitos, 19, 21 July 1989, ♀ (H. V. Weems, FSCA). BRAZIL *Amazonas:* Fonte Boa, Oct. 1975, ♂ (M. Oliveira, AMNH).

Dubiepeira lamolina new species
Figures 536–539; Map 6

Holotype. Female holotype from La Molina, 270 m, Dantas, SW of Puerto Inca, Huánuco, Peru, 30 May 1987 (D. Silva D.), in MHNSM. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace yellowish white with paired black marks, eye region black (Fig. 538). Chelicerae orange with dusky marks. Labium and sternum black. Endites dusky to black. Coxae yellowish-white; legs yellowish-white with narrow broken black rings. Dorsum of abdomen with anterior black marks, and posterior white lines separated by black bars (Fig. 538); venter with a black band (Fig. 539); sides dusky to black. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.4 diameter. Anterior median eyes 0.5 diameter apart, 0.6 from laterals. Posterior median eyes 0.4 diameter apart, 1.7 from laterals. Abdomen oval (Fig. 538). Total length 7.2 mm. Carapace 3.1 mm long, 2.3 wide. First femur 2.9 mm, patella and tibia 3.4, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.1 mm, third 1.9, fourth 2.7.

Diagnosis. This species differs from other *Dubiepeira* by having the median plate of the epigynum ventrally fused (Fig. 537). The generic assignment is uncertain.

Paratypes. ECUADOR *Napo:* Reserva Faunistica Cuyabeno, Laguna Grande, 0°00′N, 76°10–11′W, 31 July to 5 Aug. 1988, ♀ (W. Maddison 88-021, MCZ).

Dubiepeira amablemaria new species
Figures 540–542; Map 6

Holotype. Female holotype and immature paratype from Amable María, 600 m, Río Chinchamayo, Tarma Prov., Junín, Peru (K. Jelski, J. Sztolcman), in PAN. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow, only a little black pigment around eyes. Chelicerae, labium, endites, sternum, coxae, and legs yellow. Abdomen yellow-white (Fig. 542). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes slightly more than their diameter apart, 2.2 from laterals. Posterior median eyes 1.3 diameters apart, 5 from laterals. Abdomen spherical (damaged) (Fig. 542). Total length 8 mm. Carapace 3.9 mm long, 3.0 wide. First femur 4.9 mm, patella and tibia 6.6, metatarsus 5.0, tarsus 1.3. Second patella and tibia 5.4 mm, third 2.7, fourth 4.4.

Diagnosis. This species differs from others by having the median plate of the epigynum with lateral lobes (Fig. 541). The generic assignment is uncertain.

Aculepeira Chamberlin and Ivie

Aculepeira Chamberlin and Ivie, 1942: 75. Type species by original designation *Epeira aculeata* Emerton [= *Aculepeira packardi* (Thorell)]. Levi, 1977: 222.

Diagnosis. The *Aculepeira* female has an epigynum with a pointed scape (Fig. 543), a presumed apomorphic character. The tip lacks the pocket present on the tip of the *Araneus* scape. The male has a large palpus with a median apophysis bearing two flagellae on its proximal end (Fig. 547), a presumed apomorphic character, the conductor is boat-shaped to disc-shaped (in ventral view, Levi, 1977, fig. 160). The structure of the genitalia is otherwise similar to that of *Araneus*. The conductor sits on the rim of the tegulum behind the median apophysis (Figs. 547, 552), there is no paramedian apophysis, and terminal and subterminal apophyses are present, plesiomorphic characters shared with *Araneus*.

The carapace of *Aculepeira* is low, with the posterior median eyes facing up (Figs. 545, 551). (Several species placed here have the posterior median eyes facing anterolaterally [Fig. 591] and may not belong here, but the males needed for correct placement are unknown.) The abdomen in *Aculepeira* species is oval, longer than wide; some are dorsoventrally flattened (Figs. 545, 551, 556), not spherical as is typical in *Araneus*.

Note. The Neotropical species lack the ventral, median white band found in the Holarctic *Aculepeira* species and that previously was thought diagnostic (Levi, 1977); the abdomen of the Neotropical species also shows greater shape diversity than the abdomen of Holarctic species.

The males have a small embolus cap, usually two patellar macrosetae, endites with a tooth, and, in some species, a coxal hook.

The following species placed in this genus have the eyes directed anterolaterally (as in the unrelated *Eustala* and *Wixia*) and may not belong here, but the males are unknown: *aculifera*, *azul*, *busu*, *escazu*, *gravabilis*, and *visite*. The abdomen of some of these Central American and Caribbean species is more conventionally subspherical. These species all differ from *Araneus* by having a worm-shaped, wrinkled, pointed scape (Figs. 566, 578).

Natural History. The Palearctic species make a complete orb. *Aculepeira packardi* has a retreat, but some species lack it.

KEY TO FEMALE *ACULEPEIRA* FROM THE NEOTROPICS

1. Abdomen with a ventral, median, white streak, Chihuahua, Mexico (Map 7) .... *packardi*
– If ventral white markings present on abdomen, markings paired 2
2(1). Abdomen with a median, dorsal white band (Figs. 551, 562) 3
– Abdomen marked othewise 4
3(2). Abdomen length more than twice its width (Fig. 562); epigynum as in Figures 560, 561; Paraguay(?), northern Argentina .... *albovittata*
– Abdomen length less than 1.5 times its width (Fig. 551); epigynum as in Figures 548–550; São Paulo State, Brazil, to Paraguay and to Buenos Aires Prov., Argentina (Map 7) .... *vittata*
4(2). Abdomen with longitudinal bands (Fig 559); epigynum as in Figure 557; Paraguay (Map 7) .... *apa*

— Abdomen with folium or marked otherwise 5

5(4). Abdomen widest in posterior half (Figs. 545, 556); posterior median eyes facing dorsally 6

— Abdomen widest in middle or anterior half (Figs. 568, 572, 580, 598); posterior median eyes facing anterolaterally (Figs. 580, 591) 7

6(5). Width of scape less than half width of epigynum base (Fig. 543); widespread (Map 7) *travassosi*

— Width of scape more than two-thirds of epigynum base (Figs. 553, 555); Dpto. Cusco, Peru (Map 7) *machu*

7(5). Hispaniola (Map 7) 8

— Central America (Map 7) 9

8(7). Abdomen hardly longer than wide (Fig. 594), venter of abdomen with two spots (Fig. 595), epigynum as in Figures 592, 593 *visite*

— Abdomen almost twice as long as wide (Fig. 598); venter of abdomen with a pair of longitudinal white streaks (Fig. 599); epigynum as in Figures 596, 597 *busu*

9(7). In ventral view of epigynum, lateral plates of base longer than wide (Figs. 566, 578) 10

— In ventral view of epigynum, lateral plates about as wide as long (Figs. 585, 589) 11

10(9). Abdomen wider than long (Fig. 580) with one pair of ventral white spots (Fig. 584); Central America *gravabilis*

— Abdomen longer than wide (Figs. 568, 572) with two pairs of ventral spots (Fig. 569); Mexico to Guatemala (Map 7) *aculifera*

11(9). Median plate of epigynum in posterior view twice as wide as laterals (Fig. 586); Costa Rica (Map 7) *escazu*

— Median plate of epigynum in ventral view about as wide as lateral plates (Fig. 590); Panama (Map 7) *azul*

Key to Male *Aculepeira*

1 Distal end of terminal apophysis with a tooth (Fig. 565); Amazon *callaria*

— Distal end of terminal apophysis otherwise (Figs. 547, 552, 563) 2

2(1). Lateral end of median apophysis with a tooth (Fig. 563); Paraguay, Argentina (Map 7) ?*albovittata*

— Lateral end of median apophysis with a "fish tail" (Figs. 547, 552) 3

3(2). Venter of abdomen with a longitudinal median white streak; Chihuahua, Mexico (Map 7) *packardi*

— Venter of abdomen without a longitudinal median white streak 4

4(3). Abdomen with a longitudinal dorsal white band (Fig. 551); São Paulo State, Brazil, to Buenos Aires Prov., Argentina (Map 7) *lisei*

— Abdomen with a dorsal folium (Fig. 545); Mexico to Argentina (Map 7) *travassosi*

Aculepeira packardi (Thorell)
Map 7

Epeira packardii Thorell, 1875: 490. Left palpus from holotype in NHRM, examined.
Aculepeira packardi:—Levi, 1977: 228, figs. 148–161, ♀, ♂.

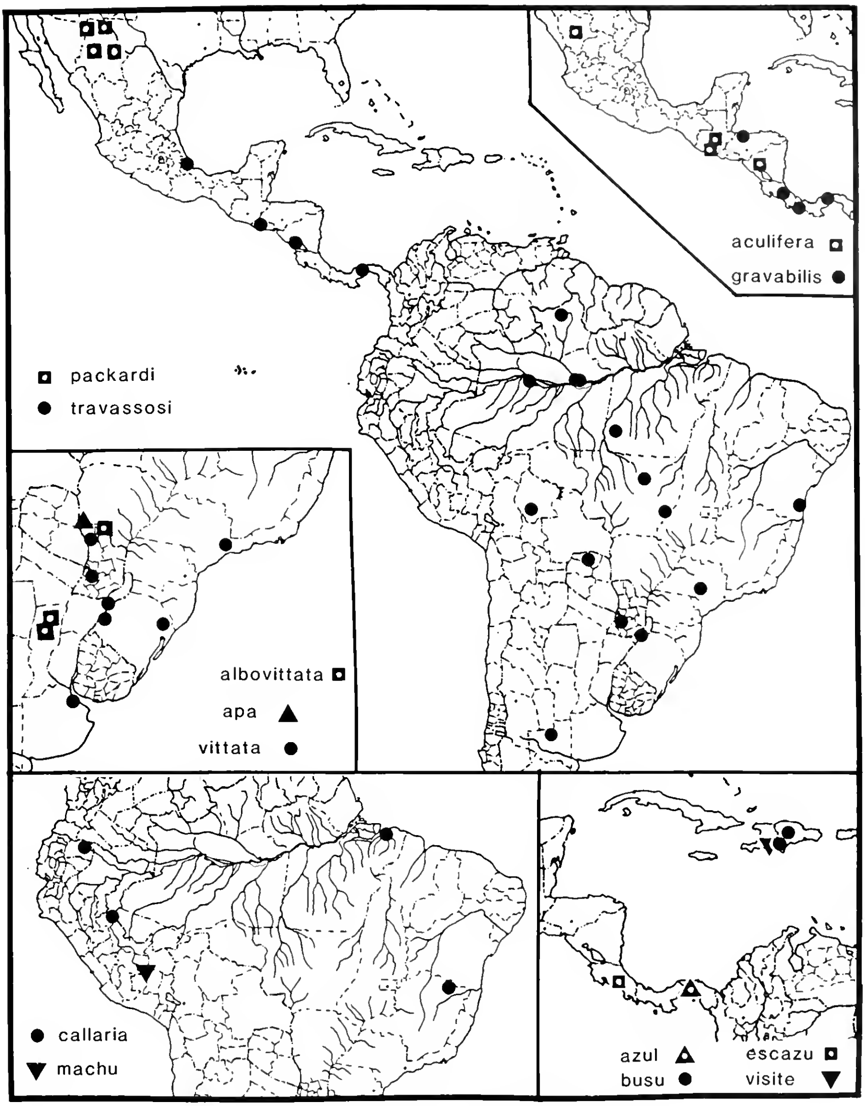
Diagnosis. Unlike the Neotropical species, this species has a white median ventral streak on the abdomen (Levi, 1977, fig. 155).

Distribution. Siberia, Labrador, western United States to Chihuahua, Mexico (Map 7).

Aculepeira travassosi (Soares and Camargo) new combination
Figures 543–547; Map 7

Neosconella travassosi Soares and Camargo, 1948: 377, figs. 33, 34, ♀. Female holotype with three paratypes from Chavantina, Mato Grosso, Brazil, in MZSP no. 1300, examined.
Neosconella cutucensis Kraus, 1955: 23, figs. 67, 69, ♂. Male holotype from sea level, Cutuco, El Salvador, in SMF no. 8503, examined. NEW SYNONYMY.
Araneus cutucensis:—Brignoli, 1983: 262.
Araneus travassosi:—Brignoli, 1983: 263.

Description. Female from Nicaragua. Carapace yellow, sides brown, sides of thorax yellow. Chelicerae marbled brown and yellow; sternum yellow, sides brown with some white pigment. Coxae yellow; legs ringed brown and yellow. Dorsum of abdomen reddish-brown with outline of dusky folium (Fig. 545). Venter black with a white U-shaped mark (Fig. 546). Posterior median and lateral eyes 0.8 diameter of anterior medians. Anterior medians their diameter apart, 1.2 diameters from laterals. Posterior medians 0.5 diameter apart, 2.2. from laterals. Abdomen oval, longer than wide, widest behind; with sclerotized discs on dorsum (Fig. 545). Total length 7.0 mm. Carapace 3.0 mm long, 2.5 wide.



Map 7. Distribution of *Aculepeira* species.

First femur 2.5 mm, patella and tibia 3.4, metatarsus 2.1, tarsus 1.1. Second patella and tibia 2.9 mm, third 2.0, fourth 2.9.

Male from Panama. Coloration as in female. Posterior median and lateral eyes 0.7 diameter of anterior medians. Anterior medians 0.7 diameter apart, 0.7 from laterals. Posterior medians 0.5 diameter apart, 1.8 from laterals. Endite with short tooth, palpal patella with two long macrosetae. First coxa with hook. Second tibia thicker than first with large distal macroseta. Abdomen elongate oval, more pointed in front than behind, with sclerotized discs. Total length 5.2 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.5 mm, patella and tibia 3.4, metatarsus 2.3, tarsus 1.1. Second patella and tibia 3.1 mm, third 1.8, fourth 2.6.

Variation. The U-shaped white marks

on the venter of the abdomen are frequently absent or may be reduced to two vertical bars. Total length of females 5.0 to 8.5 mm, of males 3.5 to 5.2. The female and male genitalia are unusually variable. While the shape of the scape is about the same in ventral view of the base, no two individuals have the outline of the plates alike.

Diagnosis. The species is separated from *A. vittata* by the distinct dorsal markings on the abdomen, with a folium containing several sclerotized paired muscle scars (Fig. 545), and from *A. machu* by the narrow scape of the epigynum (Fig. 543). There is a superficial resemblance to *Epeira carolinalis* Archer, which I placed in *Metazygia* (Levi, 1977: 94, figs. 112–117).

Natural History. Females have been collected from the canopy of a tree in an inundated forest and on low vegetation in a non-flooded forest, all near Manaus, Brazil, and on a radio antenna on the summit of Cerro Acahay in a disturbed forest in Paraguay.

Distribution. From Mexico to Argentina (Map 7).

Records. MEXICO *Veracruz:* 10 km SW Puente Nacional, 180 m, ♂, 2 imm. (G. Ball, D. R. Whitehead, R. Leech, MCZ). NICARAGUA Granada, ♀ (C. F. Baker, MCZ). PANAMA *Panamá:* Barro Colorado Isl., ♂ (A. M. Chickering, MCZ). BRAZIL *Roraima:* Ilha de Maracá, Alto Alegre, ♀ (A. Lise, INPA). *Pará:* Jacaré-Acanga, ♂ (M. Alvarenga, AMNH). *Amazonas:* Manaus, Igapó, Tarumã-Mirim, 3♀ (H. Höfer, INPA); Ilha de Marchantaria, ♀ (H. Höfer, INPA); Tefé, ♂ (H. O. Parrish, MCZ). *Bahia:* Uruçuca, ♀ (J. S. Santus, MCN 10293). *Mato Grosso:* Xingu, Jacaré, ♀ (Alvarenga, Werner, AMNH). *São Paulo:* São Paulo, Botucatu, ♀ (I. M. P. Rinaldi, L. C. Forti, MZSP). BOLIVIA *Beni:* Est. Biol. Beni, 50 km E San Borja, ♀, 2♂ (S. Larcher, USNM). PARAGUAY *Chaco:* Parque Nac. Defensores, ♀ (J. Kochalka, IBNP). *Paraguarí:* Cerro Acahay, ♀ (J. Kochalka, IBNP). ARGENTINA *Misiones:* Río Uruguai, 2♀ (E. A. Giai, MACN). *?La Pampa:* "Manantiales," ♀ (MACN).

Aculepeira vittata (Gerschman and Schiapelli) new combination

Figures 548–552; Map 7

Metepeira vittata Gerschman and Schiapelli, 1948: 17, figs. 26, 27, ♀. Female holotype from Santa María, Misiones Prov., Argentina, in MACN, examined. Brignoli, 1983: 276.

Description. Female from Vacaria. Carapace with head orange-black, thorax orange. Chelicerae, labium, endites black. Sternum orange-black. Coxae orange, first two darker; legs orange with dusky rings, first two femora black. Dorsum of abdomen with longitudinal white band (Fig. 551); venter black without markings. Posterior median eyes 0.7 diameter of anterior

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Figures 543–547. *Aculepeira travassosi* (Soares and Camargo). 543–546. Female. 543. Epigynum, ventral. 544. Epigynum, posterior. 545. Dorsal. 546. Abdomen, ventral. 547. Male, left palpus.

Figures 548–552. *A. vittata* (Gerschman and Schiapelli). 548–551. Female. 548. Epigynum, ventral. 549. Epigynum, posterior. 550. Epigynum, ventral, scape torn off. 551. Dorsal. 552. Male palpus.

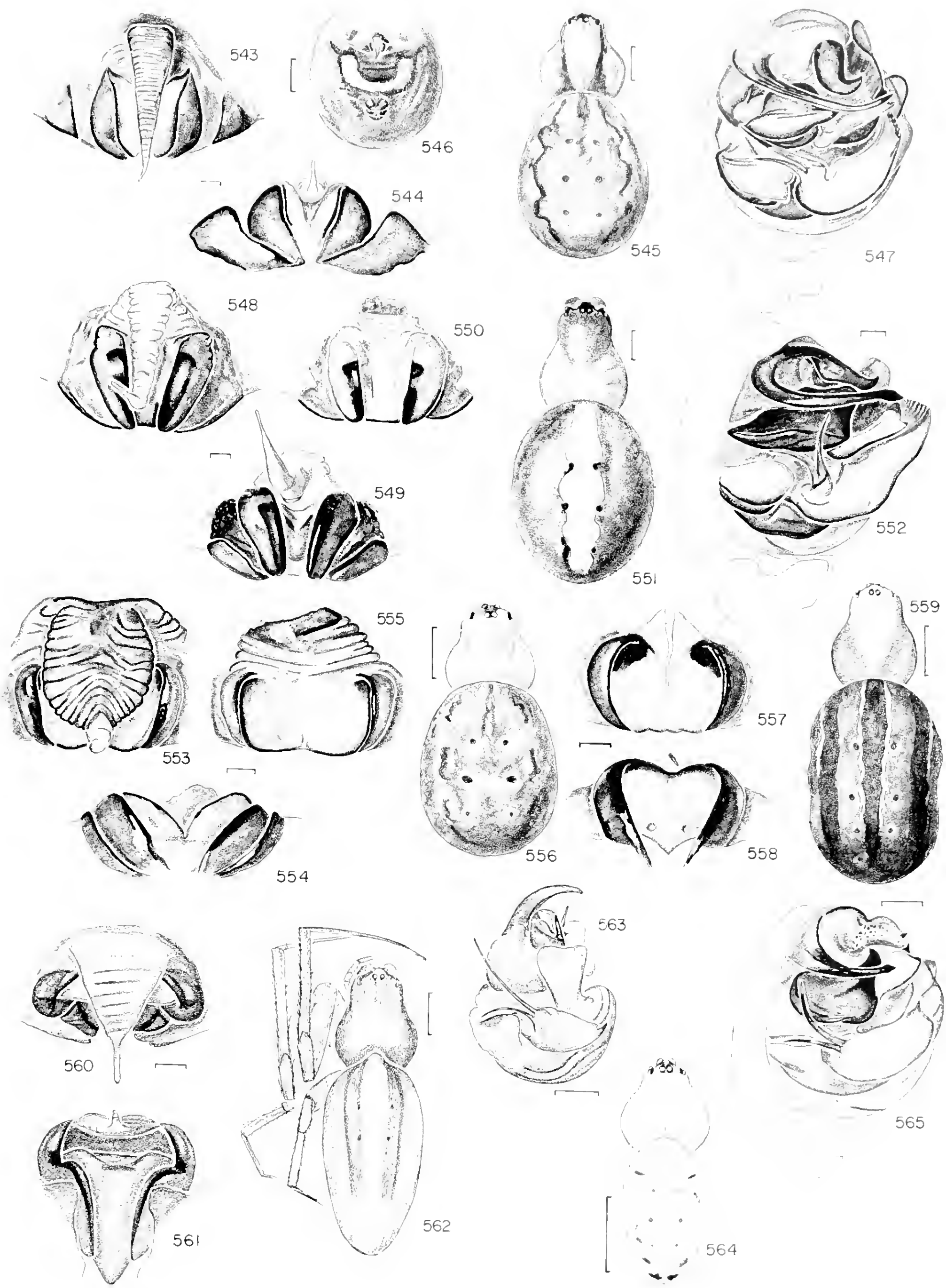
Figures 553–556. *A. machu* n. sp., female. 553. Epigynum, ventral. 554. Epigynum, posterior. 555. Epigynum, ventral, scape torn off. 556. Dorsal.

Figures 557–559. *A. apa* n. sp., female. 557. Epigynum, ventral. 558. Epigynum, posterior. 559. Dorsal.

Figures 560–563. *A. albovittata* (Mello-Leitão), female. 560. Epigynum, dorsal. 561. Epigynum, posterior. 562. Dorsal. 563. Male palpus expanded.

Figures 564–565. *A. [illegible]allara* n. sp., male. 564. Dorsal. 565. Palpus.

[illegible] genitalia 0.1 mm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medians, anterior laterals 0.7 diameter, posterior laterals 0.5. Anterior median eyes slightly more than their diameter apart, 1.3 from laterals. Posterior median eyes slightly less than their diameter apart, 3 from laterals. Abdomen oval, longer than wide (Fig. 551). Total length 10.5 mm. Carapace 4.1 mm long, 3.0 wide. First femur 2.9 mm, patella and tibia 4.0, metatarsus 2.6, tarsus 1.1. Second patella and tibia 3.7 mm, third 2.5, fourth 3.8.

Male from São Paulo. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes slightly more than 1 diameter apart, 1.2 from laterals. Posterior median eyes 0.8 diameter apart, 2.4 from laterals. Endite with minute lateral tooth, palpal trochanter with tooth. Palpal patella with two macrosetae. First coxa with small hook. Second tibia thicker than first with short and long macrosetae. Abdomen oval. Total length 6.1 mm. Carapace 3.1 mm long, 2.4 wide. First femur 2.7 mm, patella and tibia 3.7, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.5 mm, third 2.1, fourth 3.4.

Note. In living individuals the light stripe on the abdomen is yellow.

Variation. Total length of females 8.1 to 11.2 mm, of males 5.8 to 7.4.

Diagnosis. The white or yellow dorsal stripe on the black abdomen (Fig. 551) is more diagnostic than the genitalia (Figs. 548, 550, 552).

Natural History. Females in Paraguay were found in spiny umbellifers. When disturbed, they drop into the water between leaves and crawl so deep that one has to tear the plant apart. This behavior is like that of *Alpaida quadrilorata* (J. Kochalka, in letter).

Distribution. São Paulo, Brazil, to Paraguay and Buenos Aires, Argentina (Map 7).

Paratypes. BRAZIL *São Paulo:* São Paulo, Ipiranga, 26 Aug. 1941, ♀, 2♂ (B. A. M. Soares, MZSP 9654). *Mato Grosso:* ?Oct. 1976, ♀ (M. Alvarenga, AMNH). *Rio Grande do Sul:* Garruchos, S. Borja, 11 Dec. 1975, 4♀, ♂, 2 imm. (A. Lise, MCN 3155); Vacaria, 15 Jan. 1974, 7♀, 6 imm. (A. Lise, MCN 306); 21–25 Apr. 1982, ♀ (A. Lise, MCN 10238). PARAGUAY *Concepción:* Horqueta, 9 Apr. 1988, 2♀ (J. A. Kochalka, IBNP). *Paraguarí:* betw. Acahay and Cerro Acahay, 150 m, 21 Apr. 1984, ♂ (J. A. Kochalka, IBNP). ARGENTINA *Buenos Aires:* Buenos Aires, ♀ (MACN).

Aculepeira machu new species
Figures 553–556; Map 7

Holotype. Female holotype (with scape) and female paratype (with scape torn off) from Machupicchu, Cusco, Peru, ruins and bamboo-cloud forest, 2400 m, 16 Oct. 1987 (J. Coddington), in USNM. The specific name is a noun in apposition derived from the name of the type locality.

Description. Female holotype. Carapace streaky orange, darker on sides of head, glossy. Chelicerae, labium, endites, sternum orange. Coxae lighter orange; legs light orange, ringed dark orange. Dorsum of abdomen with indistinct folium (Fig. 556); venter black. Eyes subequal. Anterior median eyes slightly less than 1 diameter apart, 1.5 from laterals. Posterior median eyes 0.5 diameter apart, 2 from laterals. Abdomen oval, widest posteriorly and slightly flattened (Fig. 556). Total length 5.2 mm. Carapace 2.1 mm long, 1.8 wide. First femur 1.8 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.2 mm, third 1.3, fourth 1.9.

Diagnosis. Unlike that of *A. travassosi* (Figs. 543, 544) and *A. vittata* (Figs. 548, 549), the scape of the epigynum is wider than half the width of the epigynum base (Figs. 553, 555).

Aculepeira apa new species
Figures 557–559; Map 7

Holotype. Female holotype from Apa, Paraguay, Oct. 1908, in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace dark glossy orange. Chelicerae, labium, endites,

sternum orange. Coxae orange; legs brown with indistinct darker longitudinal lines. Dorsum of abdomen with orange, white and dark brown longitudinal bands (Fig. 559); venter black. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7. Anterior median eyes 1 diameter apart, 1.2 from laterals. Posterior median eyes 0.5 diameter apart, 2.5 from laterals. Abdomen oval (Fig. 559). Total length 6.2 mm. Carapace 2.5 mm long, 2.1 wide. First femur 2.0 mm, patella and tibia 2.8, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.5 mm, third 1.5, fourth 2.5.

Diagnosis. The small thread-like scape of the epigynum (Fig. 557) and the dorsal stripes of the abdomen (Fig. 559) distinguish this species from others.

Aculepeira albovittata (Mello-Leitão) new combination
Figures 560–563; Map 7

Neosconella albovittata Mello-Leitão, 1941b: 214, fig. 20, ♀. Female holotype from Caraguatay, Santa Fé Prov., Argentina, in MLP, examined.

Araneus melloi Brignoli, 1983: 263. New name for *Araneus albovittata*, preoccupied by Westring, 1851.

Description. Female. Carapace, sternum, legs orange. Dorsum of abdomen with a median white band indistinctly bordered by a dark band on each side; and a narrow line of red pigment between dark and white (Fig. 562). Venter with a dusky longitudinal patch, longer than wide. Posterior median eyes same diameter as anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.8. Anterior median eyes 1.3 diameters apart. Posterior median eyes their diameter apart. Abdomen elongate oval (Fig. 562). Total length 7.0 mm. Carapace 2.8 mm long, 1.8 wide. First femur 2.8 mm, patella and tibia 3.7, metatarsus 2.7, tarsus 1.3. Second patella and tibia 3.6 mm, third 2.2, fourth 2.3.

Male from Paraguay. Color as in female, abdomen with white pigment patches in median band. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 1 diameter apart, 0.6 from laterals. Posterior median eyes 1 diameter apart, 1.8 from laterals. Endite without tooth. Palpal patella with two macrosetae. First coxa without hook. First femur with six long macrosetae on prolateral side. Second tibia slightly thicker than first. Abdomen elongate oval. Total length 3.6 mm. Carapace 1.6 mm long, 1.2 wide. First femur 1.9 mm, patella and tibia 2.3, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.0 mm, third 1.1, fourth 1.8.

Note. The male from Paraguay is matched on the basis of similar structure and markings. Unfortunately its palpi are expanded (Fig. 563). The match is uncertain.

Diagnosis. The female is distinguished from other Neotropical *Aculepeira* by the elongate abdomen (Fig. 562) and by the triangular scape overhanging a transverse cavity (Fig. 560). The male has a sickle-shaped terminal apophysis (Fig. 563).

Records. PARAGUAY *Amambay:* Parque Nacional Cerro Corá, 30 Oct.–4 Nov. 1983, ♂ (J. Kochalka, MCZ). ARGENTINA *Santa Fé:* Calchaquí, Dec. 1949, ♀ (M. Birabén, MLP).

Aculepeira callaria new species
Figures 564, 565; Map 7

Holotype. Male from Colonia Callaría, Río Callaría, 15 km from Ucayali, Dpto. Ucayali, Peru, 1–16 Oct. 1961 (B. Malkin), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace light orange. Chelicerae, labium, endites orange. Sternum orange, dusky posteriorly. Coxae orange; legs dusky orange. Dorsum of abdomen light orange with an indistinct median, longitudinal band of white pigment spots and some paired dusky marks posteriorly, and a pair of black spots on posterior (Fig. 564); venter light orange. Posterior median and anterior lateral eyes 0.6 diameter of anterior medians, posterior laterals 0.5. Anterior median eyes 0.6 their diameter apart, 0.5 from laterals. Posterior

median eyes 0.3 diameter apart, 2 from laterals. Palpal patella with one seta, endite with tooth. First coxa with small hook on posterior face. Second tibia thicker than first, with macrosetae. Abdomen elongate oval. Total length 3.1 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.4, tarsus 0.7. Second patella and tibia 1.6 mm, third 1.0, fourth 1.5.

Variation. Total length 3.0 to 3.4 mm.

Diagnosis. The male differs from other *Aculepeira* males by having a spine at the tip of the terminal apophysis (Fig. 565) and from *A. albovittata* (Fig. 563) by the shape of the embolus and terminal apophysis (Fig. 565).

Paratypes. ECUADOR *Napo:* Reserva Faun. Cuyabeno, Laguna Grande, 76°10′W, 0°00′S, 1–7 Aug. 1988, ♂ (W. Maddison, MCZ). BRAZIL *Pará:* Belém, Fazenda Velha, June 1970, ♂ (M. E. Galiano, MEG). *Minas Gerais:* Pedra Azul, Dec. 1970, ♂ (P. M. Oliveira, AMNH).

Aculepeira aculifera (O. P.-Cambridge) new combination
Figures 566–577; Map 7

?*Epeira sargi* O. P.-Cambridge, 1889: 28, pl. 6, fig. 2, ♀. Female holotype from Chilascó, Guatemala, in BMNH, examined. NEW SYNONYMY.

Epeira aculifera O. P.-Cambridge, 1889: 29, pl. 7, fig. 3, ♀. Female holotype from southern slope of Volcán de Fuego, Guatemala, in BMNH, examined. Keyserling, 1892: 207, pl. 10, fig. 153, ♀.

Aranea aculifera.—F. P.-Cambridge, 1904: 512, pl. 49, fig. 5, ♀. Roewer, 1942: 836.

?*Aranea sargi.*—F. P.-Cambridge, 1904: 511, pl. 49, fig. 2, ♀. Roewer, 1942: 851.

Araneus aculifer.—Bonnet, 1955: 420.

?*Araneus sargi.*—Bonnet, 1955: 591.

Note. The holotype of *Epeira aculifera* is in poor condition, having once been pinned. The pigment and markings have been damaged as a result of poor preservation. *A. sargi* (Figs. 570–572) is probably this species but I am not certain. With a total length of 8.5 mm, *A. sargi* is slightly larger than the holotype, and it has more contrasting markings.

Description. Female holotype of *aculifera*. Carapace orange-brown, mottled. Chelicerae, labium, endites brown. Sternum dark brown with median orange streak. Coxae mottled orange to brown. Legs orange-brown, with indistinct darker rings. Dorsum of abdomen with indistinct folium (Figs. 568, 576), venter with median black band enclosing two pairs of white patches (Figs. 569, 577). Secondary eyes 0.9 diameter of anterior medians. Anterior median eyes their diameter apart, 1.5 from laterals. Posterior median eyes 1.2 diameters apart, 3 from laterals. Abdomen elongate oval. Total length 7.0 mm. Carapace 2.9 mm long, 2.3 wide. First femur 2.7 mm, patella and tibia 3.5, metatarsus 2.3, tarsus 0.9. Second patella and tibia 3.0 mm, third 1.8, fourth 2.9.

Variation. Other than the type, only three specimens were available that might belong to this species. The sclerotized plates of the epigynum are different in each of the four specimens (Figs. 567, 571, 575). The female of *A. sargi* has markings that are probably unique to that individual (Fig. 572).

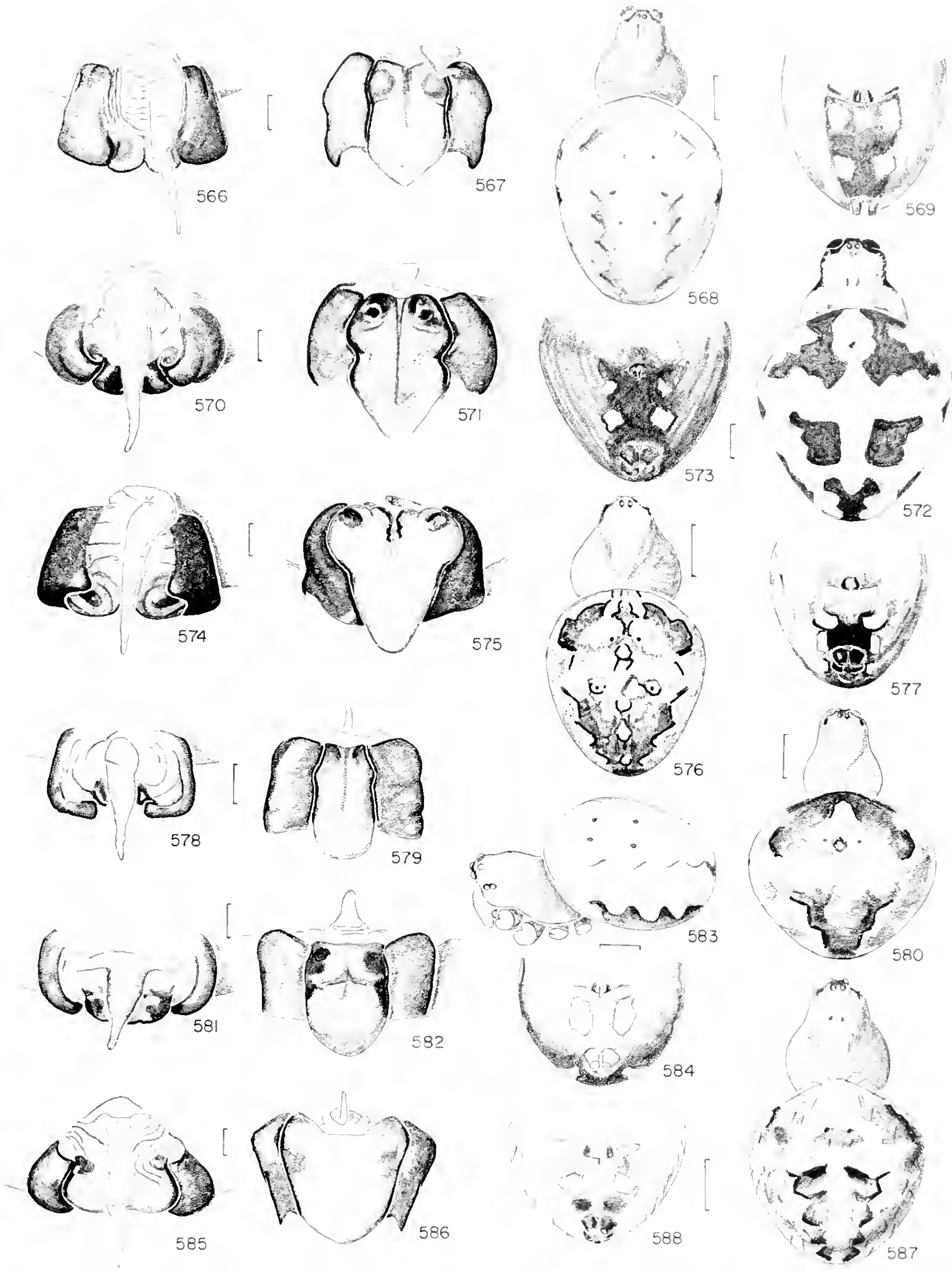
Diagnosis. This species, unlike *A. gravabilis* (Figs. 578, 581), has the scape of the epigynum folded on itself (Figs. 566, 570, 574) and the abdomen longer than wide, with four ventral white patches (Fig. 569). The placement in *Aculepeira* is tentative.

Record. MEXICO *Durango:* 16.5 km E La Ciudad, ♀ (R. E. Leech, MCZ). NICARAGUA Jinotega, 15 Aug. 1989, ♀ (F. Reinboldt, JMM).

Aculepeira gravabilis (O. P.-Cambridge) new combination
Figures 578–584; Map 7

Epeira gravabilis O. P.-Cambridge, 1889: 33, pl. 5, fig. 7, ♀. Female holotype from Volcán de Chiriquí,

Figures 566–577. *Aculepeira aculifera* (O. P.-Cambridge), females. 566, 570, 574. Epigynum, ventral. 567, 571, 575. Epigynum, posterior. 568, 572, 576. Dorsal. 569, 573, 577. Abdomen, ventral. 566–569 (holotype). 570–573 (holotype of *sargi*). 574–576 (Durango, Mexico). →



Figures 578–584. *A. gravabilis* (O. P.-Cambridge), females. 578, 581. Epigynum, ventral. 579, 582. Epigynum, posterior. 580. Dorsal. 583. Lateral. 584. Abdomen, ventral. 578, 579 (Costa Rica). 580 (Panama). 581–584 (Honduras).

Figures 585–588. *A. escazu* n. sp., female. 585. Epigynum, ventral. 586. Epigynum, posterior. 587. Dorsal. 588. Abdomen, ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.

[illegible] BMNH examined. Keyserling, 1892: 122 [illegible] 90 [illegible]
Aranea gravabilis.—Roewer, 1942: 643.
Araneus gravabilis.—Bonnet, 1955: 511.

Description. Female. Carapace, sternum, and legs orange. Dorsum of abdomen whitish and brown with brown folium (Figs. 580, 583), venter with a pair of white patches (Fig. 584). Eyes subequal. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes their diameter apart, 2.5 from laterals. Abdomen oval, wider than long, with indistinct humps (Figs. 580, 583). Total length 6.2 mm. Carapace 2.1 mm long, 1.9 wide. First femur 2.2 mm, patella and tibia 2.7, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.5 mm, third 1.3, fourth 2.0.

Variation. Total length of females 4.6 to 6.2 mm. The dorsal pattern of the abdomen is variable and one specimen from Costa Rica has the dorsum white. Each one of the specimens has a scape of slightly different shape (Figs. 578, 581).

Diagnosis. Aculepeira gravabilis differs from *A. aculifera* (Fig. 568) by having a shorter abdomen (Fig. 580) and only one pair of white spots on its venter (Fig. 584). It differs from *A. escazu* (Fig. 586) and *A. azul* (Fig. 590) by having the plates of the epigynum in posterior view about equal in width (Figs. 579, 582). The placement in *Aculepeira* is tentative.

Natural History. The female from Honduras was collected in a tree top.

Records. HONDURAS *Atlantida:* Lancetilla, July 1929, ♀ (A. M. Chickering, MCZ). COSTA RICA *San José:* Bajo Hondura, 1300 m, Mar. 1985, ♀ (W. Eberhard, MCZ). PANAMA *Chiriquí:* El Volcán, Aug. 1950, 3♀ (A. M. Chickering, MCZ). *Panama:* Cerro Jefe, 30 Dec. 1970, 2♀ (D. Quintero, MIUP).

Aculepeira escazu new species
Figures 585–588; Map 7

Holotype. Female from above Escazú, 2000 m, San José Prov., Costa Rica, Mar. 1983 (W. Eberhard 5[illegible]), in MCZ. The specific name is a noun in apposition after the type locality.

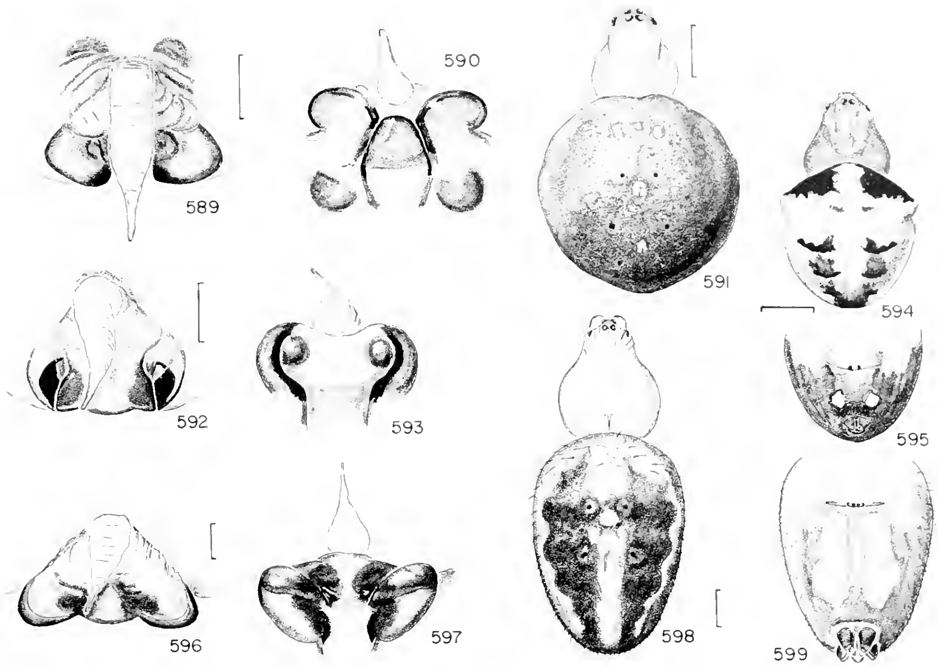
Description. Female. Carapace streaky, yellowish with white and black setae; sternum light yellowish, with brown borders. Legs yellowish with brown rings. Dorsum of abdomen contrastingly marked with a posterior folium (Fig. 587); venter with a pair of white patches side by side (Fig. 588). Posterior median eyes 1.2 diameters of anterior medians; posterior lateral eyes 0.8 diameter. Anterior median eyes 1.2 diameters apart, 2 from laterals. Posterior median eyes a little more than a diameter apart, 3.5 from laterals. Abdomen subspherical with humps (Fig. 587). Total length 5.6 mm. Carapace 2.6 mm long, 2.3 wide. First femur 3.0 mm, patella and tibia 3.6, metatarsus 2.3, tarsus 1.1. Second patella and tibia 2.9 mm, third 1.9, fourth 2.7.

Diagnosis. This species differs from *A. gravabilis* (Figs. 579, 582) and *A. azul* (Fig. 590) by having the median plate of the epigynum much wider than the lateral plates (Fig. 586). The placement in *Aculepeira* is tentative.

Aculepeira azul new species
Figures 589–591; Map 7

Holotype. Female from Cerro Azul, 600 m elevation, Ciudad Panamá, Panama, 1 Jan. 1945 (C. D., M. H. Michener), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange, eyes with abundant black pigment. Sternum dusky orange. Coxae light orange; legs dark orange, patellae lightest, tarsi darkest. Dorsum of abdomen dark orange-gray with several white spots (Fig. 591). Venter light orange-gray, with a white band on each side, connecting anteriorly; spinnerets brown, area surrounding spinnerets dusky. Posterior median eyes 1.5 diameters of anterior medians; posterior lateral eyes same diameter as anterior medians. Anterior median eyes 0.7 diameter apart, 1.3 from laterals. Posterior median eyes 0.6 diameter apart, 1.7 from laterals. Legs short. Abdomen spherical, punctate, and without hairs. Total length 5.4 mm. Carapace 2.3 mm long, 1.8 wide.



Figures 589–591. *Aculepeira azul* n. sp., female. 589. Epigynum, ventral. 590. Epigynum, posterior. 591. Dorsal.

Figures 592–595. *A. visite* n. sp., female. 592. Epigynum, ventral. 593. Epigynum, posterior. 594. Dorsal. 595. Abdomen, ventral.

Figures 596–599. *A. busu* n. sp., female. 596. Epigynum, ventral. 597. Epigynum, posterior. 598. Dorsal. 599. Abdomen, ventral.

Scale lines. 1.0 mm, genitalia 0.1 mm.

First femur 1.9 mm, patella and tibia 2.1, metatarsus 1.3, tarsus 0.8. Second patella and tibia 2.0 mm, third 1.2, fourth 1.8.

Diagnosis. This species differs from *A. gravabilis* (Figs. 579, 582) and *A. escazu* (Fig. 586) by the shape of the posterior plates of the epigynum; the lateral plates are oval (Figs. 589, 590). The placement in *Aculepeira* is tentative.

Aculepeira visite new species
Figures 592–595; Map 7

Parawixia darlingtoni Bryant, 1945: 382, fig. 21, ♀. Female only, not male holotype.
Holotype. Female holotype from La Visite, 1800–2100 m, [18°22′N, 72°12′W], Haiti, 16–23 Sept. 1934 (P. J. Darlington), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-brown, lightest between median eyes, with white setae. Chelicerae, labium, endites brown. Sternum orange, sides brown. Coxae light orange; legs orange-brown with narrow darker rings. Dorsum of abdomen white with anterolateral black patches and pairs of black patches posteriorly (Fig. 594); venter dusky with a pair of round white spots (Fig. 595). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1 diameter apart, 1.5 from laterals. Posterior median eyes 1.5 diameters apart, 2.2 from laterals. Abdomen subspherical with large anterolateral humps (Fig. 594). Total length 4.2 mm. Carapace 1.7 mm long, 1.6 wide. First femur 1.9 mm, patella and tibia 2.2, metatarsus 1.2, tarsus 0.5. Second patella and tibia 1.9 mm, third 1.1, fourth 1.6.

Diagnosis. The female differs from that

of A. busu by having two round white spots on the venter of the abdomen (Fig. 595) and by the shape of the lateral plates of the epigynum (Figs. 592, 593). The placement in *Aculepeira* is tentative.

Aculepeira busu new species
Figures 596–599; Map 7

Holotype. Female holotype and two female paratypes from Mt. Busú, 1000–1300 m, Sierra Martín García, Dominican Republic, Hispaniola, June 1983 (G. Flores, A. Gross), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange. Chelicerae, labium, endites, sternum orange. Coxae lighter orange; legs orange with indistinct brown rings. Dorsum of abdomen with brown folium (Fig. 598); venter with two white rectangles, dusky posteriorly (Fig. 599). Eyes subequal. Anterior median eyes 0.8 diameter apart, 1.5 from laterals. Posterior median eyes 0.9 diameter apart, 2 from laterals. Abdomen oval (Fig. 598). Total length 9.5 mm. Carapace 3.5 mm long, 2.9 wide. First femur 3.6 mm, patella and tibia 4.6, metatarsus 2.8, tarsus 1.3. Second patella and tibia 4.0 mm, third 2.5, fourth 4.0.

Diagnosis. This species differs from *A. visite* (Figs. 592–595) by having a longer abdomen (Fig. 598), two white rectangles on the venter of the abdomen (Fig. 599), and by the shape of the lateral plates of the epigynum (Figs. 596, 597). The placement in *Aculepeira* is tentative.

Paratypes. DOMINICAN REPUBLIC in gorge nr. Isla, nr. Hoy de Pelembito, 10 Dec. 1978, ♀ (D. G. Robinson, MNSD).

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A Review of the South American Lizard Genera *Urostrophus* and *Anisolepis* (Squamata: Iguania: Polychrotidae)

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A REVIEW OF THE SOUTH AMERICAN LIZARD GENERA *UROSTROPHUS* AND *ANISOLEPIS* (SQUAMATA: IGUANIA: POLYCHRIDAE)

RICHARD ETHERIDGE[1] and ERNEST E. WILLIAMS[2]

ABSTRACT. Lizards of the genera *Urostrophus* and *Anisolepis* represent a small, apparently monophyletic group of southern South American Iguania, placed in the family Polychridae by Frost and Etheridge (1989), and referred to informally as the "para-anoles." Para-anoles are small (70–108 mm maximum snout–vent), with a slender, moderately compressed body, and a long tail (60–77% total length). Females reach a greater maximum adult size than males, and have a slightly shorter tail, but apparently there is no sexual dichromatism. The tail is non-autotomic and has been reported to be prehensile in both species of *Urostrophus* and in *Anisolepis grilli*.

Two species of *Urostrophus* are recognized, *U. vautieri* from the Atlantic Forest of southeastern Brazil, and *U. gallardoi*, described here as new, from Misiones Province in northeastern Argentina, from the Chacoan Region of northern Argentina, and from southeastern Bolivia. Both species have smooth, flat, juxtaposed dorsal and ventral body scales, and smooth, flat subdigital scales, but the head and body scales of *U. gallardoi* are smaller and more numerous overall, and it has a larger external ear, a color pattern of greater contrast, and a smaller maximum adult size: female snout–vent length 78 mm rather than 108 mm.

Anisolepis differs from *Urostrophus* in having sharply keeled and strongly imbricate ventral body scales, a longer tail and higher number of caudal vertebrae, caudal transverse processes angled forward rather than laterally, and a higher total number of inscriptional ribs. *Anisolepis* contains three apparently allopatric species: *A. grilli*, *A. undulatus*, and *A. longicauda*, the latter formerly recognized as the only species of the genus *Aptycholaemus*, here synonymized with *Anisolepis*. The most obvious differences among the species are: the absence of a transverse gular fold and presence of a very small external ear in *A. longicauda*, distinctly heterogeneous scalation on the dorsal body and neck in *A. undulatus*, and the alternatives to these characters in *A. grilli*—a large ear, transverse gular fold, and less heterogeneous scalation.

Anisolepis grilli occurs in eastern Brazil in the Atlantic Forest and in the cultural steppe in the state of São Paulo, and in Misiones, Argentina. *Anisolepis undulatus* occurs in extreme southeastern Brazil, Uruguay, and on the south shore of the Río de La Plata in Argentina; the Uruguayan and Argentinian specimens are larger and have a different pattern than those from Brazil, but the status of the southern populations is uncertain. *Anisolepis longicauda* occurs in Paraguay and in Argentina near the western bank of the Río Paraguay and in Misiones Province, where it may be sympatric with *A. grilli*.

Published and unpublished information on various aspects of para-anole biology are included. Accounts of *Urostrophus* and *A. grilli* indicate they live in trees and bushes and are slow in their movements. There are no records of the ecology or behavior of *A. longicauda* or *A. undulatus*, but all of their known localities appear to be in a habitat of seasonally flooded grasslands (*esteros* or *bañados*), adjacent or close to a large river or lake.

One of us (RE) summarizes the long and complex history of hypotheses of para-anole relationships. There is a strong consensus that Polychridae is a monophyletic family and that *Urostrophus* and *Anisolepis* (including *Aptycholaemus*) are among its member genera, but the historical relationships of these genera to one another and to other members of the family are yet to be resolved.

INTRODUCTION

Etheridge and de Queiroz (1988), in an analysis of the phylogenetic relationships of "Iguanidae," and Frost and Etheridge (1989) tentatively recognized as monophyletic a small group of subtropical South American genera: *Urostrophus*, *Anisolepis*, and *Aptycholaemus*, and called them the "para-anoles." As the informal name implies, they show a number of resemblances to the anoles proper, a distinctive

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and clearly monophyletic group containing *Anolis*, *Chamaeolis*, *Phenacosaurus*, and *Chamaelinorops*. The para-anole genera were first linked by Etheridge in a dendrogram published by Paull, Williams, and Hall (1976), reproduced, in part, by Peterson (1983a, fig. 1b; 1983b, fig. 1), who used the term "para-anoline" for a group consisting of *Urostrophus*, *Anisolepis*, *Aptycholaemus*, and *Enyalius*. However, Etheridge and de Queiroz (1988) specifically exclude *Enyalius* from the para-anoles, placing it instead with the austral South American genera *Pristidactylus*, *Diplolaemus*, *Leiosaurus*, and *Aperopristis*, in a group termed the "leiosaurs," an action followed by Frost and Etheridge (1989). Williams (1988) included para-anoles within the leiosaurs.

Para-anoles, as we here define them, are small lizards, with a maximum snout–vent length from 70 to 108 mm. The body is slender and moderately compressed, and the slender tail represents 60 to 77% of the total length. Females attain greater maximum size than males, and have a slightly shorter tail, but there is otherwise no sexual dimorphism or dichromatism. The tail is non-autotomic and has been reported to be prehensile in some species.

Para-anoles share with other Polychridae (*sensu* Frost and Etheridge, 1989) the presence of nuchal endolymphatic sacs and midventrally continuous postxiphisternal inscriptional ribs ("chevrons"). They share with other polychrids, except *Polychrus*, the loss of femoral pores and the presence of a spinulate oberhautchen in which the spinules of the epidermal sense organs and of the subdigital scales are longer than the background spinules. With leiosaurs, para-anoles share clavicles with an angular and hooked lateral margin, and a small posterior coracoid fenestra. With anoles the para-anoles share the presence of three (rather than four) sternal ribs.

At this time, the relationships of the para-anole genera to one another (whether *Urostrophus* is monophyletic, whether the para-anoles form a monophyletic group) and their relationships with other polychrids are still in doubt; we ourselves do not agree on how to resolve these questions. Nevertheless one of us (RE) provides a summary and discussion of earlier speculations, below.

NOMENCLATURAL HISTORY

The nomenclatural history of *Urostrophus* and *Anisolepis* has been exceedingly complex, with as many synonyms as valid names. Virtually all of the descriptions, diagnoses, and accounts of distributions date from the last century and earliest part of this century, and we have found the available material to be widely scattered, frequently misidentified, mostly in South American museums, and three of the five species must still be counted as rare. Because the history of these forms has been so complex, even though published accounts are few, old, and widely scattered, we provide, below, descriptions somewhat more detailed than is usual in a work of this sort, together with what little information we have been able to accumulate on other aspects of their biology. In anticipation of our diagnosis of the genus *Anisolepis*, we point out here that the recognition of *Aptycholaemus* cannot be supported and we consider *longicauda* to be a species of *Anisolepis*.

Wiegmann (Herpetologia Mexicana, 1834) described the first species of para-anoles. He referred them to his new genus *Laemanctus*, describing three specimens in the Berlin Museum under the three names *Fitzingeri*, *undulatus*, and *obtusirostris*, differentiating them by details of color and head shape. For each of the three, the locality was "Brasilia." A fourth species, *Laemanctus longipes*, which Wiegmann described much more fully, was later made the type of that genus by Fitzinger (1843).

A further nominal species was described by Duméril and Bibron (1837) in the fourth volume of the "Erpétologie Générale," in the new genus *Urostrophus*, monotypic with the single species *vautieri*. The two

type specimens, one collected by Vautier, the other by Gaudichaud, were reported by Duméril and Bibron (1837) as having only the locality "Brasil." However, as Vanzolini (1977, p. 49) has already commented, C. Duméril (Duméril and Bibron, 1834, p. xv), in the *Discours préliminaire* to the first volume of the "Erpétologie Générale," reported that Vautier's collection was made in "Rio de Janeiro ou aux environs." One of the two syntypes in Paris is labelled "Rio de Janeiro," and this is the locality accepted for the types by Duméril and Duméril (1851, p. 55).

There was early recognition that three of the taxa named by Wiegmann were close to *U. vautieri* and distant from the fourth species, *longipes*, that Wiegmann had placed in *Laemanctus*. Fitzinger (1843) placed *undulatus* and *Fitzingeri*, along with *vautieri*, under his concept of *Urostrophus* and indeed cited *obtusirostris* only in the synonymy of *vautieri*. Gray (1845), who on page iv of his "Catalogue of Specimens of Lizards in the British Museum" mentions that he visited Berlin, among other museums, in an effort to verify species identities, placed the three Wiegmann taxa, not in *Urostrophus*, which he kept monotypic, but in his next listed genus, *Ecphymotes* Fitzinger, 1826. He distinguished *Ecphymotes* from *Urostrophus* on the basis of keeled dorsal and tail scales. This character, like the round rather than compressed tail by which he keyed out the three Wiegmann species from the fourth taxon that he referred to *Ecphymotes*, *E. acutirostris*, could only have been obtained by direct observation of the Berlin specimens. Gray is therefore the first to cite a character by which the Wiegmann types differed from *U. vautieri*, the type by monotypy of *Urostrophus*. His referral of the Berlin types to *Ecphymotes* cannot be upheld. *Ecphymotes* Fitzinger, 1826, was published as a *nomen nudum* (p. 49). In 1843 Fitzinger emended *Ecphymotes* to *Ecphymatotes* and provided a description of it as a subgenus of *Laemanctus* (p. 62). He had already on page 16 designated *Polychrus acutirostris* as the type of the genus. *Ecphymotes* thus became a strict synonym of *Polychrus* Cuvier, 1817, a phyletically distant genus. Thus, if the Wiegmann types were not referable to either *Urostrophus* or *Laemanctus*, as a result of Gray's (1845) action, they were left without a valid generic name.

Cope (1864), who had visited Berlin, and Peters (1877), who was in charge of the Berlin collection, both preferred to refer the Wiegmann species to *Urostrophus*, although Peters stressed the keeled scales of the Wiegmann types as a difference at the species level from *U. vautieri*. Boettger (1882) used the name *Laemanctus undulatus* Wiegmann for a specimen from São Paulo Province, Brasil, about which he said (translated): "A rare species. Head scales smooth but ventral scales strongly keeled, larger and more strongly keeled than those of the back." The color description, which Boettger appends, could be that of one of the specimens named by Wiegmann. On distributional grounds we believe Boettger's specimen to be the taxon that Boulenger (1891a) described as *Anisolepis grilli*.

The genus *Anisolepis* was described by Boulenger (1885a), with the sole species *A. iheringi*, on the basis of two specimens sent to the British Museum by Dr. H. von Ihering from Rio Grande do Sul, Brazil. His description was repeated and a figure published (plate IX, fig. 3, reproduced here as Fig. 7) in the second volume of Boulenger's "Catalogue of the Lizards of the British Museum (Natural History)" (Boulenger, 1885b).

In the same volume of the Catalogue, without having visited Berlin, Boulenger interpreted Gray's referral of Wiegmann's types to *Ecphymotes* and Peters' (1877) comment on keeled scales as a difference from *Urostrophus vautieri* to imply that the three names belonged in the genus *Enyalius*. He believed that he had two specimens of one of them, *Fitzingeri*, at the British Museum. He therefore based his

concept of the latter species on these, under the name *Enyalius fitzingeri*, in the process erroneously synonymizing *Enyalius undulatus* Duméril and Bibron, 1837—a mistake not corrected until noticed by Etheridge (1969). Boulenger provisionally recognized *Enyalius undulatus* Wiegmann, with *obtusirostris* as a synonym, commenting: "Although never properly characterized, this species is introduced on the authority of Peters."

In 1886, after personally examining the Berlin types, Boulenger realized that his *iheringi* was a synonym of *undulatus*, reporting the species thereafter as *Anisolepis undulatus* (Wiegmann) (Boulenger, 1886, 1887). He did not retract his reference of *Fitzingeri* to *Enyalius* and continued to synonymize *obtusirostris* with *undulatus*.

By the courtesy of Günther Peters and Rainer Günther, we have ourselves examined the Berlin types. We agree with Boulenger (1886, 1887) that *undulatus* is, indeed, the prior name of *iheringi*, but if the genus *Anisolepis* is recognized, then *Fitzingeri* and *obtusirostris*, as Etheridge indicated in 1969, are also members of that genus. Our new study shows, however, that, contrary to the opinion of Etheridge (1969), the two latter types are identical with the species which Boulenger did not describe until 1891 as *A. grilli*. We shall discuss the nomenclatural problem involved, below, under the latter name.

Having excluded Wiegmann's taxa from his concept of *Urostrophus* (relying on the character of keeled ventrals), Boulenger (1885c) in his Catalogue, on the other hand, expanded that concept to include the Chilean species *Leiosaurus torquatus* Philippi, 1861, *in* Philippi and Landbeck (1861). In so doing, as we shall show below, he was committing an error, but one at that time plausible, since he was relying on external characters that are in fact very similar in *torquatus* and *vautieri*.

Boulenger continued his error when in 1889, in redescribing Burmeister's (1861) types of *Leiosaurus scapulatus*, *L. multipunctatus* and *L. marmoratus* in the Museum at Halle, he synonymized the latter two with the first under the name *Urostrophus scapulatus*. The first two Burmeister taxa are indeed close relatives of the Chilean *torquatus*, but not of *U. vautieri*, the type of the genus; the third is now regarded as a *Liolaemus*. (See Müller, 1928, 1940, for discussion of the Burmeister types.)

On the point of confusion of *Leiosaurus* (*partim*) and *Urostrophus*, Boulenger's high authority for a long period carried the day. (Confusion had in fact begun before Boulenger, but in the reverse direction: Reinhardt and Lütken in 1861 had reported Duméril and Bibron's species from Rio de Janeiro and Lagoa Santo in Brazil as *Leiosaurus vautieri*.)

No additional species of para-anoles were described until Boulenger (1891a) described *Anisolepis grilli* from Palmeira in the state of Paraná, Brazil, and, in the same year (Boulenger, 1891b), the closely related new genus and species, *Aptycholaemus longicauda* from "Riacho del Oro, Argentina" = mouth of the Río de Oro into the Río Paraguay.

A. longicauda was the first para-anole to be discovered outside Brazil, but soon additional material turned up. In 1895 Koslowsky, of the Museo de La Plata in Argentina, referred two new species to the genus *Anisolepis*: *A. Bruchi* from Punta Lara on the south bank of the Río de La Plata in northern Buenos Aires Province, and *A. argentinus* for which the type locality was said to be "Sierra de la Ventana, cerca de Bahía Blanca," also in the Buenos Aires Province, but which Koslowsky himself, after failing to find the animal during a visit to the Sierra de la Ventana (Koslowsky, 1896), corrected to the Province of Misiones (Koslowsky, 1898).

Both Koslowsky's names were soon synonymized, *A. bruchi* with *A. undulatus* by Werner (1896) (perhaps incorrectly, see below under *A. undulatus*) and *A. argentinus* with *Aptycholaemus longicauda* by Berg (1898).

Werner himself (1896) created a syn-

onym, *A. lionotus* = *A. grilli*, from Blumenau, Santa Catarina, in Brazil, but this synonymy went long unrecognized. The name was still considered valid by Burt and Burt in 1933, and was only synonymized by Peters and Donoso-Barros (1970) on the advice of Paulo Vanzolini (confirmed by Vanzolini himself, 1977, p. 175).

The first authentic record of *Urostrophus* from Argentina was provided by Boulenger in 1902, who reported "*U. vautieri*" from Cruz del Eje, Córdoba, Argentina. Liebermann (1939) added a second locality, "Santa Fé," but without comment or mention of the museum in which the specimen was to be found.

Confusion between *Urostrophus* and the Argentinian species related to *torquatus* was at last resolved when Gallardo (1964) separated the two generic units correctly, creating for the Argentinian species *scapulatus*, mistakenly referred to *Urostrophus*, a new genus *Cupriguanus*, describing at the same time two new species in the genus, *C. achalensis* and *C. araucanus*, the latter now considered a synonym of *scapulatus* (see Etheridge and Williams, 1985). He cited in the same paper a number of records for true Argentinian *Urostrophus* as *Urostrophus vautieri*. He left, however, the position of *torquatus* uncertain, saying that it might be either *Cupriguanus* or *Leiosaurus*.

Gallardo's conclusions, although an important advance, were not entirely correct. *Cupriguanus* Gallardo, 1964, is a synonym of *Pristidactylus* Fitzinger, 1843. We report the tangled history of these two names elsewhere (Etheridge and Williams, 1985).

Gallardo was, however, quite right in recognizing *torquatus* as possibly part of the leiosaur assemblage. Peters and Donoso-Barros (1970) were, on the contrary, somewhat regressive, copying Donoso-Barros (1966) in continuing Boulenger's erroneous association of *torquatus* with *U. vautieri* and adding *U. valeriae*, a species related to *torquatus* and described by Donoso-Barros (1966) in his "Reptiles de Chile."

Prior to the present paper, then, *Urostrophus* was monotypic, all species referred to it, save *vautieri*, having been placed in *Pristidactylus* (Etheridge and Williams, 1985). Two very distinct species of *Anisolepis* are currently cited as *A. undulatus* and *A. grilli*, although there are two senior synonyms of the latter (as mentioned above). *Aptycholaemus* remains monotypic, including only *longicauda*.

In the present paper we describe and diagnose *Urostrophus* and *Anisolepis*, describing a new species of the first and synonymizing *Aptycholaemus* with the latter. Included under each species is a full diagnosis and description, with such information as we have been able to find about para-anole biology from the literature and personal correspondence. Measurements, scale counts, and skeletal characteristics are presented in tables, scale definitions are supplied in the appendix, a key is provided, and a list of specimens examined is included.

Urostrophus Duméril and Bibron 1837

1837 *Urostrophus* Duméril and Bibron, Erpét. gén., Paris, 4: 74.—Type species (by monotypy): *Urostrophus vautieri* Duméril and Bibron 1837.

Diagnosis. Urostrophus is an iguanian lizard of the family Polychridae diagnosed by the acquisition of endolymphatic sacs that extend back between the supraoccipital and parietal bones into the dorsal neck musculature, and other synapomorphies (Frost and Etheridge, 1989). *Urostrophus* differs from *Polychrus* in having lost femoral pores, from the leiosaurs (*Enyalius, Pristidactylus, Diplolaemus, Leiosaurus, Aperopristis*) in having reduced the number of sternal rib pairs from four to three and in lacking longitudinally divided distal subdigital scales, and from the anoles (*Anolis, Chamaeolis, Phenacosaurus, Chamaelinorops*) in having acquired a small posterior coracoid fenestra and in lacking elongate second ceratobranchials and the anole type digital pad. *Urostrophus* differs from *Anisolepis* (including *Ap-*

tychohalaemus, see below) in having smooth ventral scales, and posterior marginal tooth crowns with straight sides and moderate secondary cusps. The characters that distinguish *Urostrophus* from *Anisolepis* may be primitive, and the genus may be paraphyletic.

Etymology. From the Greek words *oura* meaning tail and *strophos* meaning a twisted cord, in allusion to the prehensile tail in this genus.

Characteristics. Head flat and wide.

General squamation moderately heterogeneous.

Head scales small, polygonal, juxtaposed, smooth and flat or convex, or bluntly keeled and convex.

Nasal ovoid, the nostril posterior within it or almost filling the scale, separated from the rostral by 1 postrostral, in contact with the first supralabial or separated by 1 lorilabial.

Supraorbital semicircles in contact with or separated by from 1 to 3 scales.

Supraoculars somewhat enlarged medially, in contact with the supraorbital series or not; a circumorbital series complete or not.

Interparietal suboval, larger than the other scales of the area, which are usually not differentiated, separated from the semicircles by 1 to 3 scales and from the nape granules by 5 to 8 scales. Parietal eye present.

Canthals 3 to 4, oriented toward the nasal, the anteriormost separated from it by 1 to 2 scales.

Superciliaries 11 to 16, squarish, or the first or first 3 elongate and oblique.

Loreals 8 to 27, varying much in size.

Lorilabials in 1 to 2 rows, partly or completely separating the subocular scale or scales from the supralabials. One or 2 rows continue forward on a labial shelf to below the nasal.

Supralabials 6 to 10, the fifth to eighth below the center of the eye.

Preoculars 1 to 3, the uppermost usually in contact with the first canthal.

Subocular single, elongate or broken into 2 to 4 scales, rarely in contact with supralabials, usually separated by 1 to 2 rows of lorilabials.

Postoculars variable, not well differentiated.

Lower temporals larger or smaller, smooth, flat or convex. An intertemporal line or zone of enlarged scales not or weakly indicated.

Ear variable, from subround to vertically oval, from slightly smaller than interparietal to as much as three times larger. Anterior margin of ear beaded or not, posterior margin granular.

Mental triangular to pentagonal, in contact with 2 postmentals (=first sublabials) between infralabials. One to 5 sublabials on each side in sequence with the first sublabials.

Central gulars smooth, convex, separated by minute granules, grading posteriorly into large imbricate smooth scales.

Transverse gular-antehumeral fold present. A pregular fold present or not.

Nape folds ill-defined. A longitudinal fold sometimes distinguishable.

Middorsals smooth, flat or slightly convex, partly separated by minute granules, none enlarged into a median row, but variable in size.

Nape scales smaller than dorsals, granular, smooth.

Body slightly to noticeably depressed.

Flank scales smooth or very bluntly keeled, separated by minute granules, variable in size.

Ventrals much larger than any dorsal or flank scales, smooth, imbricate or subimbricate, in transverse rows. Scales at anterior border of vent granular.

Tail somewhat compressed, without verticils.

Caudal scales granular at base and smooth, becoming larger, hexagonal, keeled, and imbricate distally.

Tail less than 76% of total length.

Limb scales smooth, largest in front of thigh, varying from granular to imbricate and separated by minute granules or not.

Supradigitals of hand smooth, imbricate, often wide, lamella-like. Supradigitals of foot smooth, imbricate, narrower

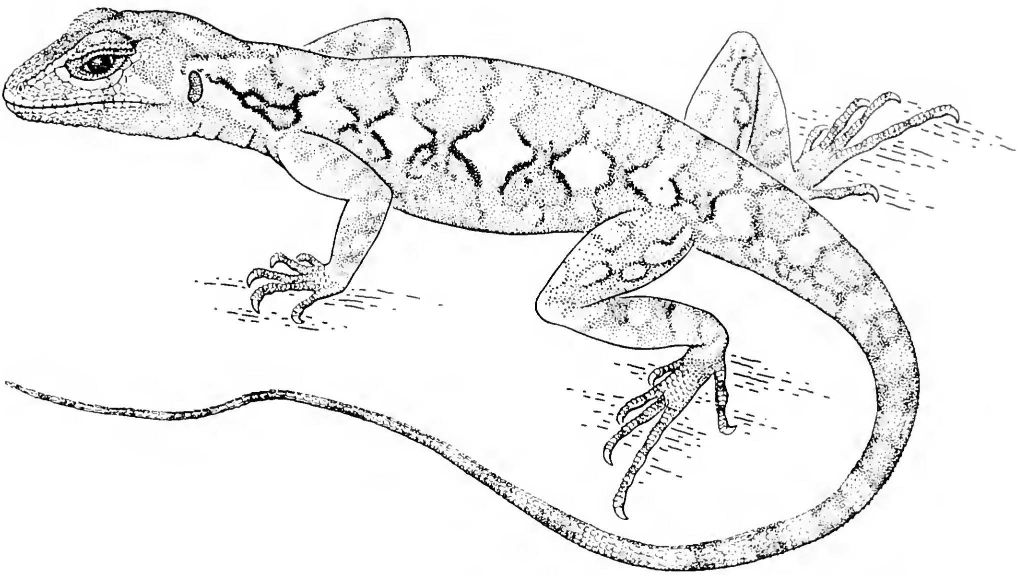


Figure 1. *Urostrophus gallardoi,* MACN 4311.24, adult male 70 mm snout–vent length, from Rosario de la Frontera, Argentina.

than those of hand. Infradigitals of both hand and foot smooth, imbricate, wide, lamellar.

No femoral or preanal pores.

Axillary pocket distinct to obscure. An inguinal pocket never present.

Urostrophus gallardoi new species
Figures 1 and 2; Tables 1–4

1902 *Urostrophus vautieri*—Boulenger, Ann. Mag. Nat. Hist., London, (7)9: 337.

1939 *Urostrophus vautieri*—Liebermann, Physis, Buenos Aires, 16: 66.

1960 *Urostrophus vautieri*—Hellmich, Abh. Bayer, Akad. Wiss. (N.F.), 101: 48.

1964 *Urostrophus vautieri*—Gallardo, Neotropica, Buenos Aires, 10(33): 126.

1979 *Pristidactylus vautieri*—Gallardo, Monogr. Mus. Nat. Hist. Univ. Kansas, Lawrence, 7: 302.

1981 *Urostrophus vautieri*—Laurent and Teran, Misc. Inst. M. Lillo, Tucumán, 71: 11.

1984 *Urostrophus vautieri*—Bee de Speroni and Cabrera, Rev. Mus. Argent. Cien. Nat. "Bernardino Rivadavia," Zool., 8(10): 115.

1985 *Urostrophus gallardoi* (*nomen nudum*)—Laurent, Nat. Geogr. Soc. Research Rept., 1977 projects, p. 422.

1986 *Urostrophus vautieri*—Cabrera and Bee de Speroni, Historia Natural, 6, p. 8.

1986 *Urostrophus vautieri*—Cei, Monographie IV, Mus. Reg. Sci. Nat. Torino, p. 175, footnote.

Holotype. Mus. Argent. Cien. Nat. No. 11043, Urundel, Dept. Oran. Prov. Salta, Argentina (23°43′S-64°47′W). J. Crespo, collector.

Paratypes. ARGENTINA: *Córdoba:* Cruz del Eje, BMNH 1902.5.22.4. *La Rioja:* Aimogasta (possibly in error fide R. Laurent in litt.), MZUSP 45908. *Salta:* El Quebrachal, ABarrio 746; Quebrada Río Las Conchas, FML 01266; Río Chuña Pampa (=Chuñapampa), about 10 km WNW La Viña, FML 01296; Puesto San Borja, Sierra de Metán, 15 km W Metán, FML 00847; Rosario de la Frontera (city), MCZ 162922, MACN 4311–24 (1 specimen); 35 km N Cafayate, MCZ 162920, MACN 12016. *Santa Fé:* no additional data, MACN 19740. *Santiago del Estero:* Santiago del Estero (city), MACN 8019–21; outskirts of Santiago del Estero, ABarrio 121; Bandera, ABarrio 345. *Tucumán:* no additional data, MACN 4318–25 (1 specimen); Dept. Burruyacú, no additional data, FML 00483. BOLIVIA: *Santa Cruz:* Santa Cruz de la Sierra, MACN 2786–88.

Etymology. Named in honor of José Maria Gallardo, who first correctly distin-

guished *Urostrophus* from *Cupriguanus* = *Pristidactylus*, and also briefly described the characteristics of the Argentine population.

Diagnosis. Differs from *U. vautieri* in having smaller scales (i.e., higher scale counts, see Tables 2 and 3), a larger external ear opening, much larger than the interparietal scale, and a more distinct color pattern, with regular crossbands and usually a fully ringed tail. In large adults the upper head scales and underlying dermal skull roof rugosities are more convex.

Description. Head (Fig. 2). Head scales small, smooth, polygonal, convex, becoming swollen and sometimes keeled in large adults. Rostral subpentagonal, about two or three times as wide as high. Five or 6 postrostrals. Nasal ovoid, nostril in posterior dorsal position or almost filling scale, in contact with the first supralabial, separated from the rostral by the lateral postrostral or in very narrow contact. Five to 8 scales between the nasals dorsally. Frontonasal scales small, smooth (or swollen), polygonal, varying greatly in size, 7 to 11 between the posterior canthals. Eight to 13 supraorbitals in an arc on each side, the semicircles separated medially by 2, rarely 1 or 3 scales that are only slightly smaller than the scales of the semicircles themselves. Supraoculars enlarged medially (the largest may be transversely oriented), usually separated from the semicircles by a complete circumorbital series. Six or 7 scales across the supraocular area from the supraorbitals to the superciliaries. Scales of parietal region small, smooth (or swollen), varying greatly in size. Interparietal nearly oval, separated from the semicircles by 1 to 2 scales on each side, separated from the nape scales by about 5 scales. Canthals 3 to 4, the anteriormost separated from the nasal by a much smaller scale. Superciliaries 11 or 12, all squarish except the first, or first 2 which may be elongate; none overlapping. Loreals varying much in size, 11 to 18. Two rows of lorilabials, only 1 extending beneath the subocular. One preocular on each side. Subocular single, elongate. Postoculars not well differentiated from the temporals. Supralabials 7 to 10, separated from the subocular by one row of lorilabials or rarely in contact, the sixth, seventh, or eighth below the center of the eye.

Temporals small, smooth, slightly convex, variable in size, 11 to 14 between orbit and ear. A very indistinct intertemporal area of slightly enlarged scales separating upper and lower temporals. Anterior auriculars like lower temporals but more convex, hence anterior margin of ear "beaded." Posterior auriculars granular. Ear vertically oval, usually two to three times the size of interparietal.

Mental pentagonal, in contact with 2 polygonal postmentals between the infralabials. One to 4 sublabials on each side in sequence with the postmentals; only the postmentals in contact with the infralabials. Infralabials 8 to 13. Central gulars granular, smooth, convex, subimbricate, often partially separated by minute granules, grading posteriorly into larger distinctly imbricate smooth scales just in front of the gular fold. Antehumeral-transverse gular fold distinct. A pregular fold at best vaguely indicated. Lateral nape folds not well defined.

Body. Middorsals subgranular, smooth, convex, subimbricate, or partially separated by minute granules, irregular in size. No trace of a vertebral scale row. Nape scales smaller than middorsals, granular, smooth, separated by minute granules. Flank scales granular, smooth, separated by minute granules, varying in size. Ventrals much larger, smooth, imbricate, subhexagonal, in transverse rows. Scales at anterior margin of vent subgranular.

Limbs. Brachials: all upper forelimb scales smooth, convex, and separated by minute granules, some as large as dorsals but infrabrachials and axillary scales granular. Antebrachials: all lower forearm scales smooth, convex, but the more distal become larger and more imbricate and only the more proximal retain minute granules between them. Carpals: supra-

carpals smooth, strongly imbricate. Infracarpals smooth, not as large or as strongly imbricate. Digitals of hand: supradigitals weakly tectiform, imbricate distally, wider than long or not. Infradigitals smooth, imbricate distally, wider than long proximally, narrower on the distal part of the toe except for the 3 most distal scales, which are again wider than long. Axilla granular with minute granules interspersed. No axillary pit.

Femorals: suprafemorals larger than dorsals, smooth. Prefemorals larger to much larger than dorsals, largest near knee and subimbricate to imbricate. Infrafemorals like prefemorals but smaller and less distinctly imbricate. Postfemorals granular with minute granules between. Tibials: supratibials like dorsal scales but sometimes subimbricate. Pretibials and infratibials enlarged, imbricate. A granular zone at the ankle joint dorsally. Tarsals: supratarsals smooth, imbricate like pre- and infratibials. Infratarsals swollen, smooth, imbricate. Digitals of foot: supradigitals smooth, imbricate distally, not wider than long. Infradigitals smooth, imbricate distally, wider than long proximally or not wider than long, narrower distally. Lamellae under fourth toe 22 to 29.

Groin granular. No inguinal pit.

Tail. Base of tail scaled like body, the more distal scales becoming larger both above and below, and 4 to 7 ventral rows always distinctly keeled, and the dorsal and lateral scales becoming keeled after the proximal third of tail length.

Color and Pattern. (Fig. 1). The color pattern of *Urostrophus gallardoi*, at least in preservative, appears to be quite uniform, and that of a paratype (MCZ 162922) is typical: Ground color pale yellowish gray brown. On dorsum and nape a pattern of brown darker edged rhombs, two dorsolateral, two on midflanks. These connected transversely by broad bridges into crossbands that have boldly undulant borders anteriorly and posteriorly. Continuing onto the distal tail these bands become paler and with straighter edges and extend

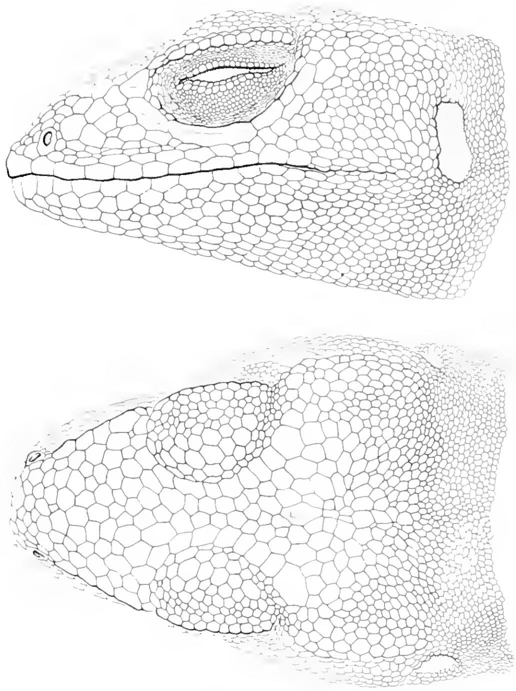


Figure 2. Head scales of *Urostrophus gallardoi*, MACN 4311.24, adult male, from Rosario de la Frontera, Argentina: Top, left lateral. Bottom, dorsal.

around the tail as full rings. Limbs above more vaguely patterned in brown and yellow gray. Belly, throat and undersides of limbs very vaguely and weakly patterned.

According to Gallardo (1964, translated): "Its coloration is light brown with seven darker transverse bands with rhomboidal figures on the dorsum of the trunk; the tail is ringed with dark." Bee de Speroni and Cabrera (1984, translated) describe a specimen from northern Córdoba Province as follows: "Dorsally yellowish gray with markings of dark gray almost black, arranged transversely in the form of irregular rhombs, six from neck to anus, and 20 on the tail, there continuing ventrally as rings. On the arms and legs the dark color predominates over the white like diffuse spotting. . . . Ventrally the color is pale yellowish gray sprinkled with black dots on the throat, arms and legs. The coloration coincides with previous descriptions

(e.g., Gallardo, 1964), except that this specimen does not possess a black but a whitish palate, and the axillae and the internal border of the mouth are yellow, a fact not reported by other authors." That the latter description is from a live specimen is confirmed by Cabrera (in litt.). He states, comparing coloration of the Cordoba specimen in life with our Figure 1, that the dorsal and limb patterns are darker, the light spaces in between having scattered brown spots, and emphasizes again that the axillae and borders of the mouth are yellow and brighter than the pale yellowish gray of the background. He further describes the ventral color in life as pale yellowish gray with small dark brown spots, scattered or sometimes forming a network on the throat. Under the throat and under the arms, where the scales are granular, the brown spots are almost central and many times larger than the scale itself, while ventrally under both body and limbs, where the scales are larger and smooth, the spots are scattered, fewer, and situated at the edges of the scales.

Gallardo's (1964) report of a black palate and throat in *U. gallardoi* is in agreement with Duméril and Bibron's (1837) description of the palate of *U. vautieri*, which Rand (in litt.) has confirmed (see below). However, Cabrera (in litt.) restates and amplifies the description in Bee de Speroni and Cabrera (above), remarking that in *U. gallardoi* the oral mucosa that covers the vomer, palatines, and more anterior part of the pterygoid bones is white, and only becomes black in the throat. He comments that when the lizard opens its mouth it is hard to see the black surface. (The anterior palate of the MCZ paratype of *U. gallardoi* from Salta, Argentina, has been compared with the anterior palate of an MCZ specimen of *U. vautieri* from São Paulo, Brazil. The first is unpigmented, the second is black.)

Distribution. (Map 1). Known in Argentina from the provinces of Córdoba, Misiones, Santa Fé, Tucumán, Santiago del Estero, and Salta, and in Bolivia from Santa Cruz de la Sierra. A record from Aimogasta, La Rioja Province, Argentina, is questionable (R. Laurent, in litt.). The specimen from Misiones (Universidad Nacional de Córdoba AC 079) is widely separated from the localities in the Chacoan Region of northern Argentina and Bolivia, but Cabrera (in litt.) has compared it with specimens from Córdoba and confirms its identification as *U. gallardoi.*

Reproduction. Gallardo (1964) states that a female from Salta collected in December contained seven eggs; another contained five eggs, 16 × 8 mm, with a yellowish-white membranous shell.

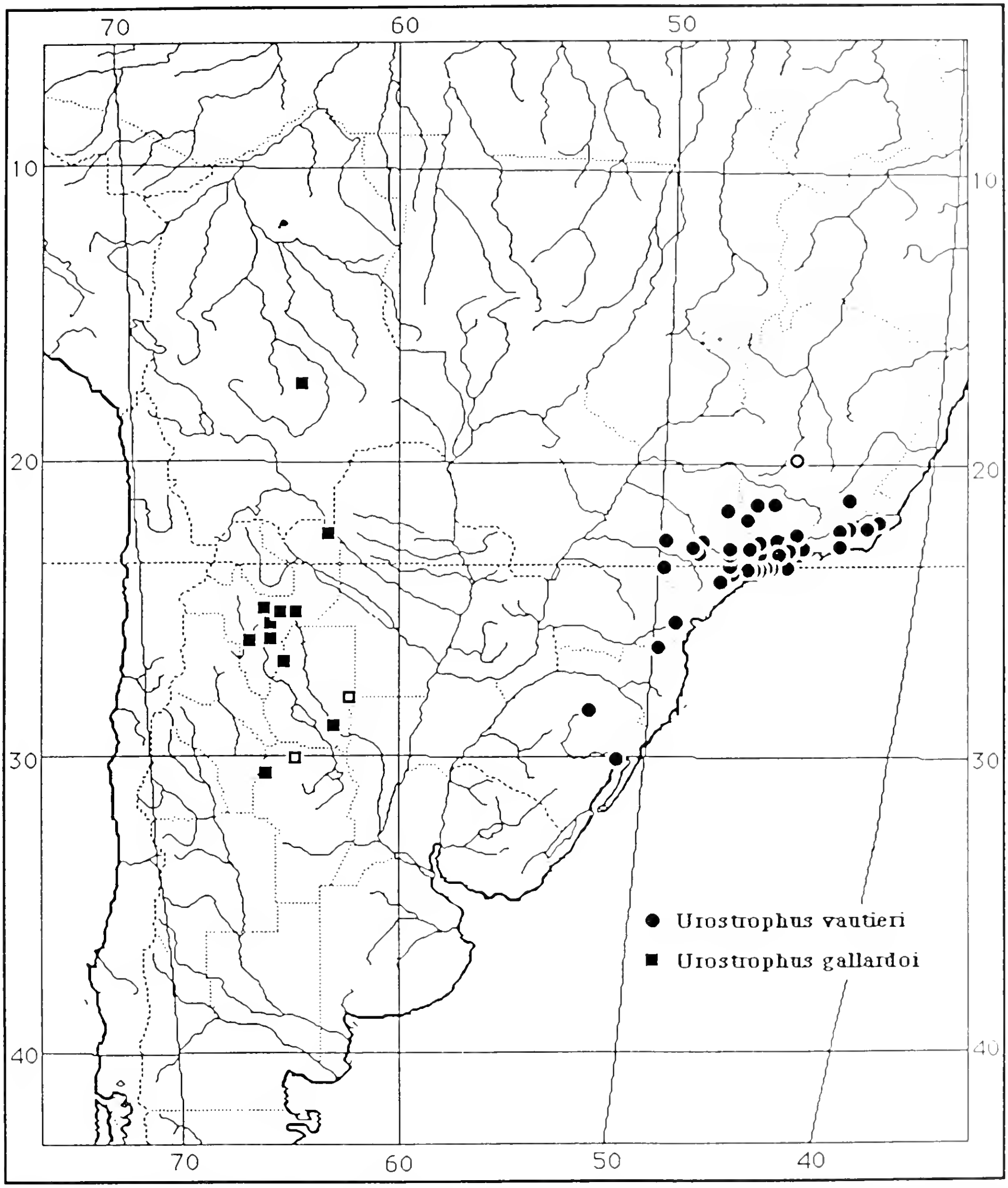
Behavior. The tail is partly prehensile according to Bee de Speroni and Cabrera (1984).

Ecology. Gallardo (1979) lists this species, under the name *Pristidactylus vautieri,* as an endemic of the Argentinian Chaco, and in figure 12 of the same work, which diagrams the "structural habitat" of lizards in an arid chacoan landscape, he places it on the trunk of a small, low tree, at the same height as *Aperopristis paronae* on an adjacent tree, and with *Tropidurus spinulosus* and *Tropidurus* sp. (=*T. etheridgei*) occurring both above and below the perch of *U. gallardoi.* Bee de Speroni and Cabrera (1984) say that the cryptic coloration of *U. gallardoi* imitates quite well the trunks of the trees with lichens (*Prosopis, Acacia*) that are common in the zone where the species is found, allowing them to pass unnoticed, an observation quite parallel to that of Gallardo (1977) for *Anisolepis grilli* that we record below. In a list of the herpetofauna of the province of Tucumán, Laurent and Teran (1981) indicate the occurrence of this species (as *U. vautieri*) in the eastern part of the province in "Bosques chaqueños . . . 250–500 (750) m" and "Bosque de transición . . . 350–700 m."

Urostrophus vautieri Duméril and Bibron 1837

Figure 3; Tables 1–4

1837 *Urostrophus vautieri* Duméril and Bibron, Erpét. gén., Paris, 4: 78; 8: pl. 37, fig. 1.—Type locality: "Brésil."—Restricted type locality (Duméril and Duméril, 1851): "Rio-Janeiro." (Syntypes: Mus. Hist. Nat. Paris 6779, 6780.)



Map 1. The distribution of *Urostrophus gallardoi* (squares) and *Urostrophus vautieri* (circles). Solid symbols represent localities from which specimens were seen by us.

1843 *Laemanctus (Urostrophus) Vautieri*—Fitzinger, Syst. Rept., Wien, 1: 62.
1845 *Urostrophus (lapsus) vautieri*—Gray, Cat. Liz. Coll. Brit. Mus., London, 184.
1851 *Urostrophus vautieri*—Duméril and Duméril, Cat. Méth. Coll. Rept. Mus. d'Hist. Nat. Paris, 55.
1862 *Leiosaurus vautieri*—Reinhardt and Lütken, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn, 1861: 223.
1868 *Urostrophus vautieri*—Hensel, Arch. f. Naturgesch., 34(1): 348.
1885 *Urostrophus vautieri*—Boulenger, Cat. Liz. Brit. Mus., London, 2: 122.

Diagnosis.—Differs from its only congener, described above, in having larger scales overall (i.e., lower scale counts, see

Tables 2 and 3), a smaller external ear opening, smaller than the interparietal scale, and a less distinct color pattern, characteristically lichenate, with the tail banded above but not fully ringed. The head scales and the underlying dermal skull roof rugosities are not as distinctly convex in large adults.

Etymology. Named for L. L. Vautier, collector of one of the syntypes.

Description. Head (Fig. 3). Head scales small, smooth, polygonal, flat or convex. Rostral pentagonal, two to three times as wide as high. Four to 6 postrostrals. Nasal ovoid, nostril almost filling scale, separated from rostral by 1 to 2 scales, from first supralabial by 1. Six scales between nasals. Five to 8 scales between posterior canthals. Supraorbital semicircles narrowly in contact or separated by 1 scale as large as those of the semicircles. Supraoculars enlarged medially, the largest oriented transversely, separated from the semicircles by a complete circumorbital series or this series incomplete. Four scales across supraocular area between supraorbitals and superciliaries.

Interparietal oval, separated from the semicircles by 1 to 2 scales on each side, from the nape scales by 3 to 7 scales. Canthals 2 to 4, the anteriormost often oriented obliquely upward, separated from the nasal by a much smaller scale or in contact. Superciliaries 10 to 14, the first largest, the first 1 to 3 oblique, the remainder squarish. Loreals very variable in size, 9 to 22. One row of lorilabials which extends beneath the suboculars. One to 2 preoculars. Suboculars 1 to 3, elongate. Postoculars not well differentiated from the temporals, except for the lowermost, which is distinctly larger. Eight to 9 supralabials, the fifth or sixth below the center of the eye, separated from the subocular by 1 row of lorilabials.

Temporals small, flat or slightly convex, variable in size, about 9 to 11 between orbit and ear. No distinct area of enlarged scales between upper and lower temporals. Anterior auriculars like temporals but smaller and slightly convex. Anterior margin of ear not distinctly "beaded." Posterior auriculars granular. Ear subround to vertically oval, not or not much larger than interparietal.

Mental pentagonal, wide, in contact with 2 transversely oriented postmentals between the infralabials (sometimes also with lateral gulars, symmetrically or asymmetrically). Two to 4 sublabials in sequence with the postmentals, but only the postmentals in contact with the infralabials (or even the latter excluded by lateral gulars). Infralabials 6 to 8. Central gulars granular, smooth, partially separated by minute granules, grading posteriorly into larger, distinctly imbricate scales just anterior to the gular fold. Antehumeral-transverse gular fold distinct. A pregular fold often present. Lateral nape folds very ill-defined.

Body. Middorsals subgranular, smooth, slightly convex, juxtaposed or partly separated by minute granules, rather irregular in size. No trace of a vertebral scale row. Nape scales smaller than middorsals, granular, smooth, separated by minute granules. Flank scales smooth, granular, somewhat variable in size, separated by minute granules, and in almost regular transverse rows. Ventrals larger, smooth, not imbricate, partly separated by minute granules, in transverse rows.

Limbs. Brachials: all upper forelimb scales smooth, some as large as dorsals, convex, and separated by minute granules. Antebrachials: all lower forelimb scales smooth, and flat or slightly convex, the most distal distinctly imbricate and only the most proximal retaining minute granules between them. Carpals: supracarpals smooth, flat, imbricate. Infracarpals smooth, juxtaposed or weakly imbricate. Digitals of hand: supradigitals smooth, more or less wrapping around the digits, wider than long proximally, less so distally. Infradigitals smooth, wider than long and relatively flat proximally, the intermediate scales narrower and wrapping around the digit, the 3 distal scales again wider than long and wrapping around the digit. Axilla granular with minute granules interspersed. No axillary pit.

Femorals: suprafemorals larger than

dorsals, smooth, juxtaposed. Prefemorals larger than dorsals, smooth, subimbricate to imbricate, not significantly larger at knee. Infrafemorals like prefemorals but smaller. Postfemorals granular with minute granules between. Tibials: supratibials the size of dorsals, smooth with minute granules between. Pretibials and infratibials enlarged, smooth, subimbricate or imbricate. A granular zone at the ankle dorsally. Tarsals: supra- and infratarsals smooth, imbricate. Digitals of foot: supradigitals smooth, subimbricate, not wider than long. Infradigitals smooth, wider or not wider than long proximally, narrower distally. Lamellae under fourth toe 23 to 32.

Groin granular with minute granules interspersed. No inguinal pit.

Tail. Base of tail scaled like body, but more distal scales becoming slightly larger both above and below, and rectangular or trapezoidal. Six ventral rows becoming keeled just beyond the base of the tail and all caudal scales after about the proximal third of tail length.

Color and Pattern. The color pattern in preserved animals is variable but seems always to be weakly defined. Description of MZUSP 4462 from Garça, São Paulo, exchanged to San Diego State University, will serve for comparison with color in life as described below:

"Greyish, very vaguely mottled with brown above. Lines of dark pigment in the sutures of many head scales. On the side of the head two oblique dark rays across the orbit, one angled toward the ear, the other onto the posterior labials. Vague irregular brownish rhombs on the dorsum in front of hind limbs. More distinct rhombs on tail just posterior to hind limbs, continuations of these distally becoming fainter and assuming the character of dorsal bands. Below belly, throat, undersides of limbs and tail white without pattern."

A. S. Rand (notes taken in São Paulo in 1963 and 1964, generously provided) has the only description of *U. vautieri* in life, all from caged animals. He records one animal as having the general appearance

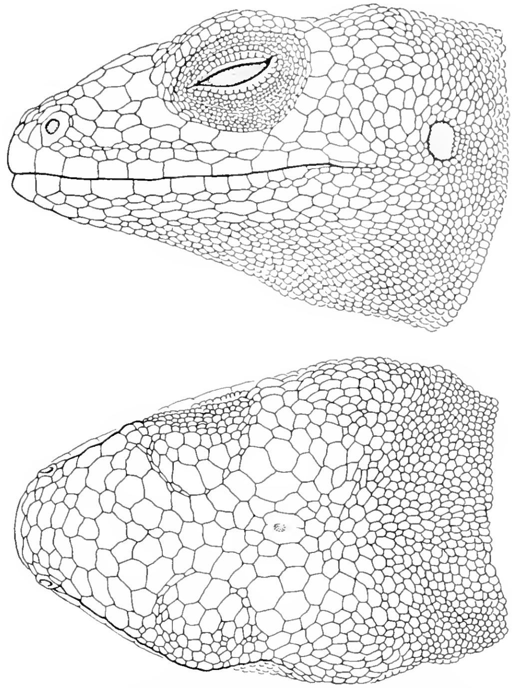


Figure 3. Head scales of *Urostrophus vautieri*, MCZ 84037 from Serra Negra, Brazil: Top, left lateral. Bottom, dorsal.

of a lichenate stick, the throat and roof of mouth black, tongue, lips, and mouth pink, and the body as "grey mottled with brown, sometimes taking a definite greenish tint. The mottling is heaviest on the neck and back and less on the sides. The tail is banded with brown (not ringed)."

Another lizard is described as "brown with dark brown markings dorsally. Head above light grey-brown with several narrow dark markings. A narrow dark brown line across head at anterior border of orbits. Another line behind this on each side running posterodorsally to meet its fellow at the interparietal scale. Posterior margin of head marked by a narrow transverse band broken at the midline and with several short anterior extensions. Some of the sutures between the head scales are also dark. The side of the head below and in front of the eye light grey-brown. Orbit brown with several dark markings radiating from it, two dorsally to connect with

the lines on the top of the head, one extending backward as a dark band extending a short distance toward the ear. Body light brown with a series of seven cross-bands or saddles, irregularly shaped and reaching down onto the sides and there breaking up, middorsally widening so as to connect longitudinally or nearly so. The middorsal centers of the saddles light brown like the areas between and around them. Saddles continued onto the tail. Legs light brown cross-banded with darker. Below light brown with many scattered darker scales. The animal sometimes grey and sometimes with a greenish cast."

Distribution. (Map 1). The Atlantic Forest of eastern Brazil in the states of Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and south of the Atlantic Forest in northern Rio Grande do Sul; no records are available from the intervening state of Santa Catarina. A record from "Paraguay" may be in error.

Behavior. Rand's notes include comments on behavior, again on caged animals. We abstract them here:

U. vautieri is slow-moving, indeed moves less than *Polychrus acutirostris* and is immobile for long periods. Like *Polychrus* the head is held straight out from the body which is held close to and parallel to the supporting branch. The tail is definitely prehensile, and the animal can hang by the tail but does not do so unless compelled by being pushed off its perch. It can then turn around and pull itself up to the supporting branch. In climbing, the tail is used as a holdfast; in jumping, the tail is used upon landing. The tail coils slowly.

A brief display was seen by one animal in response to an *Enyalius* that shared its cage and which it chased about: A slow full up movement of the head, a slow movement down, then quick up and down. Body compressed, throat gorged.

Commenting on eye movement, Rand remarks, "The eye in this species has a light greyish iris with a pair of brownish areas on each side. These spots permit the observation that when the head is tilted upward, the eye rotates in such a way that it retains its position relative to the horizontal."

Reproduction. Rand (1982) removed clutches of fully shelled eggs from the oviducts of five individuals measuring 68 to 86 mm snout–vent length. Clutch size varied from 6 to 13 (M = 9.6), egg volume from 0.5 to 0.7 ml (M = 0.6), and clutch volume from 3.1 to 8.3 ml (M = 5.5). One of us (RE) counted 5 eggs in the right oviduct and 7 in the left in a female (MZUSP 36114) measuring 78 mm snout–vent length.

Karyotype. M. L. Beçak *et al.* (1973) report a karyotype of 2n = 36 (12 macrochromosomes and 24 microchromosomes). This pattern is regarded as primitive for lizards (Gorman, 1973; Paull, Williams, and Hall, 1976) and conveys no information about the species' affinities.

Miscellaneous. Pessôa and de Biasi (1973) report a plasmodium in the blood of *Urostrophus vautieri.*

Anisolepis Boulenger 1885

1885 *Anisolepis* Boulenger, Ann. Mag. Nat. Hist., London, (5)16: 85.—Type species (by monotypy): *Anisolepis iheringi* Boulenger 1885 = *Laemanctus undulatus* Wiegmann 1834.

1891 *Aptycholaemus* Boulenger, Ann. Mag. Nat. Hist., London, (6)8: 85.—Type species (by monotypy): *Aptycholaemus longicauda* Boulenger 1891.

Diagnosis. Anisolepis is a member of the iguanian family Polychridae, diagnosed by the acquisition of endolymphatic sacs that extend back between the supraoccipital and parietal bones into the dorsal neck musculature and other synapomorphies (Frost and Etheridge, 1989). It differs from *Polychrus* in having lost femoral pores, from the leiosaurs (*Enyalius, Pristidactylus, Diplolaemus, Leiosaurus, Aperopristis*) in having reduced the number of sternal rib pairs from 4 to 3 and in lacking longitudinally divided distal subdigital scales, and from the anoles (*Anolis, Chamaeolis, Phenacosaurus, Chamaelinorops*) in having acquired a small posterior coracoid fenestra, and in lacking

elongate second ceratobranchials and an anole type digital pad. *Anisolepis* differs from *Urostrophus* in having keeled ventral scales, and posterior marginal tooth crowns with tapered sides and reduced secondary cusps.

Etheridge and de Queiroz (1988) listed as derived characters shared by *Anisolepis undulatus*, *A. grilli*, and *Aptycholaemus longicauda* the reduction in secondary cusps of the marginal tooth crowns, loss of the posterolateral processes of the basisphenoid, and the acquisition of a ventrolateral row of enlarged scales and ventral body scales with sharp keels in parallel rows. *Aptycholaemus* was diagnosed by loss of the transverse gular fold, elongation of the tail, and reduction of the external ear. However, there are no derived features known to be shared by *undulatus* and *grilli* to the exclusion of *longicauda*, and therefore no evidence that *undulatus* and *grilli* share a more recent common ancestor with each other than with *longicauda*. Accordingly we here place *Aptycholaemus* Boulenger 1891 in the synonymy of *Anisolepis* Boulenger 1885. Thus constituted, *Anisolepis* is probably monophyletic.

Etymology. From the Greek *anisos* meaning unequal and *lepis* meaning scale, with reference to the heterogeneity of the squamation.

Characteristics. General squamation moderately to strongly heterogeneous.

Head scales small, polygonal, juxtaposed, smooth, flat or swollen.

Nasal round to flask-shaped, nostril posterodorsal or nearly filling scale, separated from the rostral by a postrostral, in contact with the first supralabial or separated by a lorilabial.

Supraorbital semicircles usually separated by 1 or 2 scales, rarely in contact or separated by 3.

Supraoculars rather weakly enlarged medially, in contact with supraorbitals or not, the circumorbital series differentiated or not.

Interparietal round or vertically oval, larger than the other scales of the area, which are usually not differentiated, separated from the semicircles by 1 to 3 scales and from the nape granules by 5 to 8 scales. Parietal eye present.

Canthals 3, the anterior often angled above the nasal from which it is separated by a granule.

Superciliaries 7 to 10, the anterior 2 to 5 overlapping strongly posteriorly, the remainder with vertical sutures.

Loreals 11 to 31, varying much in size.

Lorilabials in 1 to 2 rows, completely or partly separating the subocular from supralabials. One to 2 rows continue forward on a labial shelf, to or below nasal.

Supralabials 6 to 10, the seventh to ninth below the center of the eye.

Preoculars 1 to 3, the uppermost in contact with the first supralabial and first canthal, or with first canthal only.

Subocular single, elongate, rarely in contact with the supralabials, usually separated by 1 to 2 rows of lorilabials.

Two to 4 differentiated postoculars or these indistinct.

Lower temporals smooth or weakly keeled. An intertemporal line or zone of enlarged scales present.

Ear subround, small and oblique, smaller than interparietal; or oval, equal to or larger than interparietal. Anterior margin like adjacent temporals, beaded, posterior margin granular.

Mental subpentagonal, wider than high, in contact with 2 postmentals (=first sublabials) between the infralabials or with these and a small median scale (=median gular). One to 7 sublabials in sequence on each side with the first sublabials.

Central gulars smooth and juxtaposed, rarely weakly keeled and subimbricate, becoming larger and imbricate, smooth or keeled just before the transverse gular fold or posteriorly always large, keeled and imbricate, continued without change into the keeled ventrals.

Transverse gular-antehumeral fold present or absent. Pregular fold present or absent.

Longitudinal nape fold present, well defined by the enlarged scales, or indistinct and without distinctly enlarged scales.

Middorsals irregular in size, weakly to strongly keeled, flat or swollen, in a distinct zone or not, the vertebral rows smaller than the paravertebrals or not. No middorsal row of aligned scales.

Nape scales granular or subgranular, grading into keeled dorsals. Two lines of enlarged scales on lateral nape or not.

Flank scales smaller but irregular in size, keeled or smooth, separated by minute granules or not, with 1, 2, or no longitudinal, partial or complete lines of enlarged scales that are keeled and imbricate. Granular areas in axilla and groin.

Ventrals much larger, strongly keeled, imbricate, mucronate or submucronate. Scales at anterior margin of vent smaller, less strongly keeled or subgranular.

Tail more or less compressed, all scales keeled, imbricate. Ventral scales of tail may be larger than body ventrals. Verticils not present.

Tail greater than 69% of total length.

Limb scales imbricate, keeled anteriorly, granular on posterior of humeri and femora, sometimes with minute granules grading into keeled scales dorsally. Ankle and inside of knee also granular.

Supradigitals of hand wide, imbricate, smooth, or uni- or multicarinate. Supradigitals of foot narrower, imbricate, weakly keeled or multicarinate.

Infradigitals of both hand and foot wide, smooth, imbricate, sublamellar.

No femoral or preanal pores.

Axillary pocket present or absent. No inguinal pocket.

Anisolepis grilli Boulenger 1891

Figures 4, 5, and 6; Tables 1–4

1834 *L. [aemanctus] obtusirostris* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46.—Type locality: "Brasilia." (Holotype: Zool. Mus. Berlin No. 496).*

1834 *L. [aemanctus] Fitzingeri* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46.—Type locality: "Brasilia." (Holotype: Zool. Mus. Berlin No. 495).*

1837 *Laemanctus Fitzingeri*—Duméril and Bibron, Erpét. gén., Paris, 4: 74.

1837 *Laemanctus obtusirostris*—Duméril and Bibron, Erpét. gén., Paris, 4: 75.

1843 *Laemanctus (Urostrophus) Fitzingeri*—Fitzinger, Syst. Rept., Wien, 1: 62.

1845 *Ecphymotes Fitzingeri*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London: 184.

1845 *Ecphymotes obtusirostris*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London: 185.

1882 *Laemanctus undulatus*—Boettger, Ber. Senckenberg. Naturf. Ges., 130.

1891 *Anisolepis grilli* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2)10: 909.—Type locality: "Palmeira, Province of Paraná, Brazil." (Syntypes: Brit. Mus. Nat. Hist. Nos. 91.11.19.2 [RR 1946.8.12.38], 91.9.24.10 [RR 1946.8.5.58]).

1893 *Anisolepis undulatus*—Boettger, Kat. Rept.-Samm. Senckenberg, 1: 61.

1896 *Anisolepis lionotus* Werner, Verhandl. Zool. Bot. Ges. Wien, 46: 470.—Type locality: "Blumenau, Provinz Sta. Catarina, Brasilien." (Holotype: Naturhist. Mus. Wien No. 18904).

1896 *Anisolepis grilli*—Werner, Verhandl. Zool. Bot. Ges. Wien, 46: 471.

1905 *Anisolepis undulatus*—Boettger, Zool. Anz., 29(11): 373.

1930 *Aptycholaemus longicauda*—Burt and Burt, Proc. U.S. Nat. Mus., 78(6): 7.

1961 *Anisolepis grilli*—Capocaccia, Ann. Mus. Civ. Stor. Nat. Genova, 72: 92.

1965 *A. [nisolepis] iheringi*—Etheridge, Herpetologica, 21(3): 167.

1965 *A. [nisolepis] lionotus*—Etheridge, Herpetologica, 21(3): 167.

1970 *Anisolepis grilli*—Peters and Donoso-Barros, Bull. U.S. Nat. Mus., 297: 42. (*A. lionotus* synonymized.)

1976 *Anisolepis iheringi*—Gundy and Wurst, J. Herpet., 10(2): 116.

1982 *Anisolepis undulatus*—de Queiroz, Herpetologica, 38(2): 310.

Diagnosis. A. grilli differs from *A. undulatus* in having less distinctively heterogeneous scalation: enlarged dorsal body scales grading gradually into smaller flank

* Although these names have priority over the name *Anisolepis grilli* Boulenger 1891, neither have been used since Gray (1845). At least five authors in ten [illegible] have used Boulenger's *A. grilli* to refer to this species during the past 50 years, which, according to Article 79c of the International Code of Zoological Nomenclature (1985) provides a prima facie case for suppression of the two Wiegmann names in favor of Boulenger's *A. grilli*. Accordingly we are applying to the International Commission on Zoological Nomenclature for suppression of *L. obtusirostris* and *L. Fitzingeri*.

scales rather than being abruptly larger, nape without enlarged, erect scales, no dorsolateral rows of enlarged, keeled scales, supradigital scales of hand smooth rather than indistinctly uni- or multicarinate, keeled ventral scales in more (17 to 25 versus 13 to 19) longitudinal rows, and a larger adult size (maximum snout–vent length of females 97 mm, males 79 mm, versus females 83 mm, males 70 mm). *A. grilli* differs from *A. longicauda* in having a larger external ear, larger than the interparietal scale rather than conspicuously smaller, in having an antehumeral-transverse gular fold, and a shorter tail (mean tail/total length in males 0.73, females 0.71, versus males 0.77, females 0.74).

Etymology. Named after Dr. G. Franco Grillo, collector of the syntypes.

Description. Head (Fig. 4). Head scales small to moderate, smooth, swollen, variable in size. Rostral subpentagonal, twice to about three times as wide as high. Postrostrals 6 or 7. Nasal ovoid, nostril slightly posterior in position, in contact with the first supralabial or separated from it by 1 scale, separated from the rostral by 1 post-

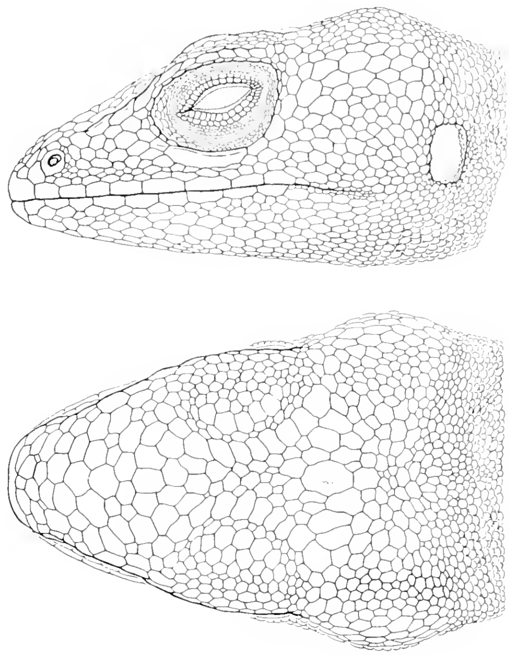


Figure 4. Head scales of *Anisolepis grilli*, MCZ 133190 from Dorizon, Paraná, Brazil: Top, left lateral. Bottom, dorsal.

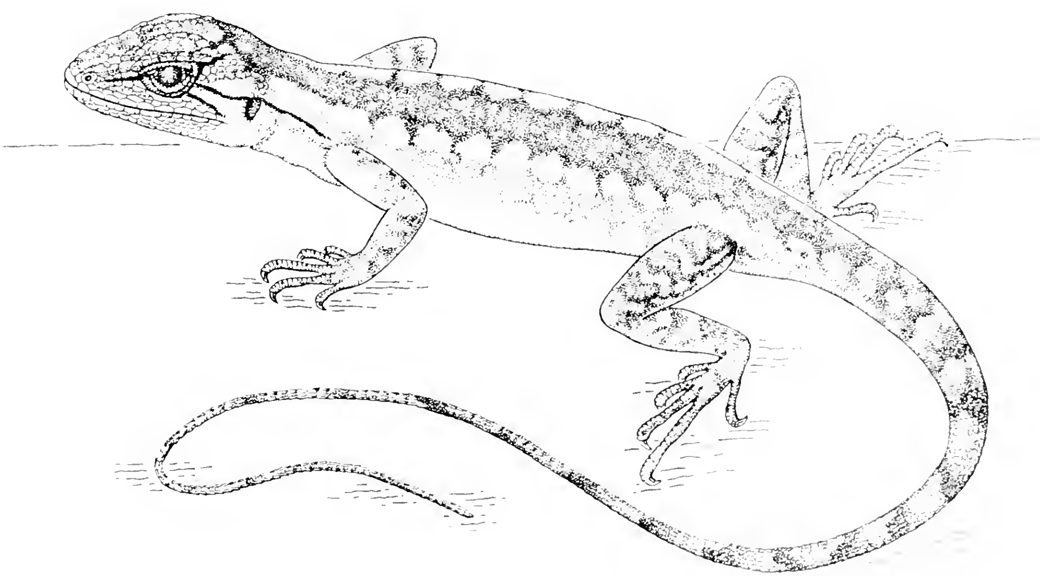


Figure 5. *Anisolepis grilli*, NMW 18904, holotype of *Anisolepis lionotus*, from Blumenau, Santa Catarina, Brazil.

rostral. Six to 7 scales between the nasals dorsally. Frontonasal scales moderate, smooth, polygonal, relatively uniform in size. Six to 10 scales between the posterior canthals. Supraorbital semicircles separated medially by 1 to 4 scale rows. Supraoculars enlarged medially, the largest scales tending to be transversely oriented. A circumorbital series separating supraorbitals and supraoculars, complete or not. Four to 6 scales across the supraocular region between the supraorbitals and the superciliaries.

Scales of parietal region smaller than those of the frontonasal region, smallest anteriorly and posteriorly, largest laterally. Interparietal larger than surrounding scales, nearly oval, separated from the semicircles on each side by 1 to 3 scales, from the nape granules by 5 to 7 scales. Canthals 2 to 4, the anteriormost obliquely positioned partly above the nasal from which it is separated by a scale or granule, or with which it is in contact. Eight to 11 superciliaries in 2 rows, the first largest, the first 3 to 5 slightly elongate, the remainder squarish or rectangular, those anterior in the lower row overlapping more strongly those in the upper row. One to 2 preoculars, in contact with the posterior canthal or separated from it by a polygonal scale. Suboculars 1 to 2. Two to 4 postoculars, not very distinct from the temporals. Loreals 25 to 39, very variable in size. Two rows of lorilabials below the loreals, a complete or incomplete row extending below the subocular, separating it from the supralabials. One anterior lorilabial inserted below the nasal. Ten to 11 supralabials, the sixth or seventh below the center of the eye.

Temporals small, somewhat variable in size, about 11 between orbit and ear. A single or double line of enlarged scales or no such line differentiated. Anterior auriculars smaller than temporals, and anterior margin of ear weakly "beaded." Posterior auriculars granular. Ear vertically oval, larger than or equal to interparietal.

Mental pentagonal, wide, in contact with 2 transversely positioned postmentals (=first sublabials), rarely also narrowly in contact with a lateral gular on one or both sides. Two to 3 sublabials in sequence with the first sublabials. Six to 9 infralabials. Central gulars smooth, juxtaposed or sometimes with granules between, becoming larger, keeled and imbricate in front of the transverse gular fold.

Antehumeral-transverse gular fold distinct. A pregular fold often present.

Body. About 6 to 9 middorsal rows of small, keeled scales, irregular in size, juxtaposed, tending to grade into flank scales, which are smaller but also irregular in size, keeled and partly separated by minute granules. A ventrolateral line of enlarged scales ca. 6 scales above the ventrals or this line absent. Nape scales, juxtaposed or separated by granules, smaller than middorsals, swollen, keeling weak or absent. No lines of enlarged scales on nape. Ventrals larger, keeled, the keels not in line, imbricate, mucronate, in about 21 to 25 transverse rows.

Limbs. Brachials: suprabrachials rather large, keeled, imbricate. Infra- and postbrachials subgranular, imbricate or granular, juxtaposed or with minute granules between. Antebrachials: keeled, imbricate above; below imbricate, generally smaller and only some scales keeled. Carpals: supracarpals imbricate, keeled. Infracarpals imbricate, smooth. Digitals of hand: supradigitals imbricate, smooth or weakly uni- or bicarinate, wider than long. Infradigitals imbricate, smooth, wrapped around digit. Axilla granular. Axillary pit present, deep or shallow.

Femorals: suprafemorals keeled, imbricate, variable in size, smaller at knee. Postfemorals granular with minute granules between. Tibials: keeled, imbricate all around. A granular zone dorsally at ankle.

Tarsals: supratarsals keeled, imbricate. Infratarsals smooth, swollen, imbricate.

Digitals of foot: supradigitals keeled, at least as wide as long, imbricate. Infradigitals smooth, wider than long, imbricate.

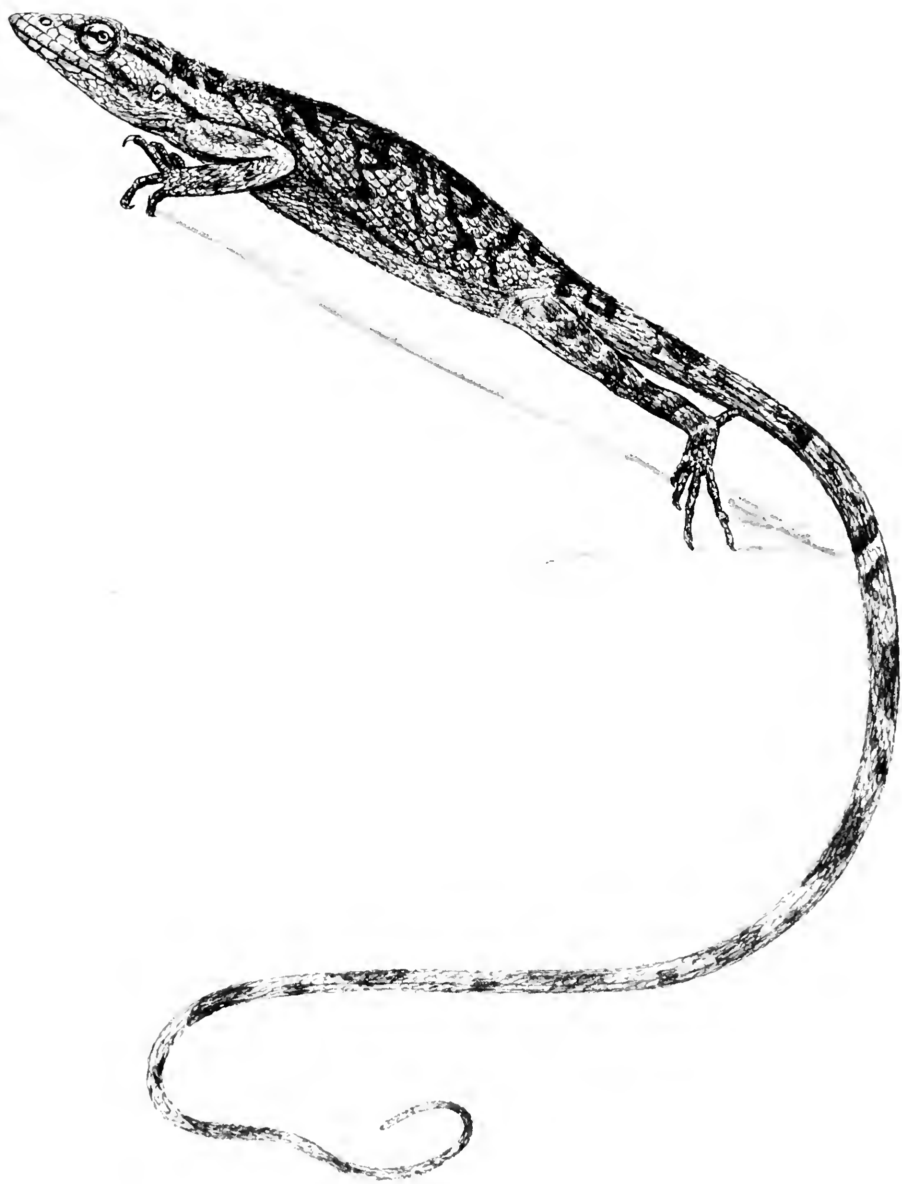


Figure 6. Sketch of *Anisolepis grilli* done by a São Paulo artist from the living animal and donated by A. S. Rand.

Twenty-nine to 33 lamellae under fourth toe. Groin granular. No inguinal pit.

Tail. All caudal scales keeled, the keels in line, ca. 4 ventral rows larger.

Color and Pattern. (Figs. 5, 6). The color pattern in preserved animals is highly variable; gray or brown may predominate. Boulenger's (1891a) color description ap-

pears to represent a decidedly reduced pattern, as Werner (1896) has already commented: "Purplish brown above, with some rusty spots, loreal region and lips bluish gray, the throat whitish, the rest of the lower parts pale brown."

More frequently the pattern, as again Werner (1896) commented, may be quite similar to that of *A. undulatus* as figured by Boulenger (1885c) for a syntype of *A. iheringi*. We describe such a pattern below from MZUSP 10142 from São Bernardo, São Paulo, exchanged to San Diego State University.

"Color composed of browns, light browns, dark browns, grey browns and grey. Head above dark brown. Laterally a light brown stripe with irregular margins extending from the posterior orbit onto nape above ear. Light brown on labials continued backward to lower edge of ear and flecked with darker scales. Body middorsally with a broad brown band continuous forward with the dark brown of the head, edged laterally with darker triangles, apices ventral, which are each continued ventrolaterally by narrow irregular dark lines that are bordered anteriorly by wider lines of grey and posteriorly by light brown oval areas. The grey and dark brown lines join on the lower flanks a ventrolateral band, grey mottled with dark brown. This ventrolateral band is itself continued ventrally by grey and dark brown lines like those above, but more vertical, and like the upper lines enclosing light brown spots, but these more random. Belly light brown vaguely streaked with grey. Throat light brown with sparse fine dark spotting. Underside of limbs light brown mottled and smudged with grey. Tail above like dorsum at base but dorsolateral band fading into the light lateral color of the distal tail which is very lightly smudged with darker."

Rand (1964 notes on São Paulo caged specimens) reports the color in life of a female *Anisolepis grilli*:

"Brown above with a definite darker dorsal pattern. Head above medium brown with indistinct dorsal mottling and scattered lighter scales. Sides of head, loreal region, lips and lower jaw light brown or yellowish brown, with scattered dark brown scales. An indistinct dark line starting at the anterior border of the orbit, broken by the eye, continuing to the posterior margin of the orbit, there forking with a narrow branch going posteriorly to the upper half of the anterior border of the ear, broken by ear, then proceeding onto neck almost to the level of the shoulder. Iris golden.

"Body with a middorsal stripe, about 10 or 12 scales wide, of medium grey brown, margined by a series of dark triangles, apices lateral, bases merging into the dorsal stripe. The triangles start at the back of the head as irregular dark spots close together (or an interrupted dark band). These spots take on their triangular shape just behind the level of the shoulders, alternating from side to side, so close-set that their bases seem to touch, about 11 on each side from shoulder to base of tail. The tips of the most distinct triangles are surrounded by white or tan light spots and are extended posterolaterally by dark lines reaching about halfway down the flanks, to about the level of the ear and the upper face of the hindleg. The upper parts of these dark lines are the most distinct and are edged by the same light color that emphasizes the tips of the triangles. On the neck this light color is seen as a light line margining the dark nape band laterally. The areas between the dark triangles and the lines, as well as the lower flanks, are light brown, flecked with small dark markings.

"The dark triangles extend onto the proximal three-fourths of the tail, becoming saddles separated by light brown. The legs above are, like the lower flanks, light brown flecked with darker. The venter is light brown, becoming yellow midventrally on the belly and the chest and chin, the latter and the throat with black or dark brown scales not arranged in any pattern. The undersides of legs and tail are light brown. The tongue and the lip pale pink, the inside of mouth and throat black."

Another female specimen is described as "like the first in pattern but the brown areas darker, almost a slaty grey, and the light areas a pinkish or reddish brown. The belly is distinctly flecked with dark and like the light areas in ground color."

Still another specimen differs only slightly: "The lizard a grey brown, speckled or mottled with lighter. The top of the head is grey with lighter grey flecks; the side of the head has a light stripe from the eye, including the upper eyelid, back to the temple, light brown below this and then a dark grey band through the eye, above the ear and onto the neck. Underneath this the loreal region, the upper part of the eye, the lips and back through the ear are light brown like the throat.

"The back has a light grey brown dorsal stripe, edged with the bases of black triangles. These point laterally; their bases do not meet but are separated by about their own length. From the tip of each triangle a black streak with irregular margins extends down and back at about a 45° angle less than halfway down the side. The triangles and lines are edged behind by light tan patches. The ground color is a medium grey flecked with dark. There is an indistinct series of light spots in a line from the axilla to the groin. The black triangles alternate.

"The dorsal black markings continue on the tail, where they meet at midline and for the posterior two-thirds of the tail form irregular cross bands. The legs have irregular light and dark cross bands on a grey ground.

"The venter is light, lightest in the midline and flecked with black.

"The pupil is round, the iris light brown."

Distribution. (Map 2). Known in Brazil from the states of Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, where it occurs in the Atlantic Forest, but also in "cultural steppe" in the state of São Paulo (Vanzolini, 1983). Recorded in Argentina from the Misiones Province. Two specimens (Zool. Mus. Berlin 6246) are said to have come from Montevideo, Uruguay. The locality seems doubtful, but if accurate, *A. grilli* may be sympatric with *A. undulatus* in Uruguay.

Behavior. Rand (notes of 1963 and 1964) reports that *A. grilli* like *U. vautieri* has a fully prehensile tail, can hang by it and pull itself back up to its perch, but, like *vautieri*, it does not do so willingly. The tail of *grilli* curls immediately on contact with a perch; it is used as a hook not a hand. Again, like *vautieri*, *grilli* may be immobile (in cages) for long periods.

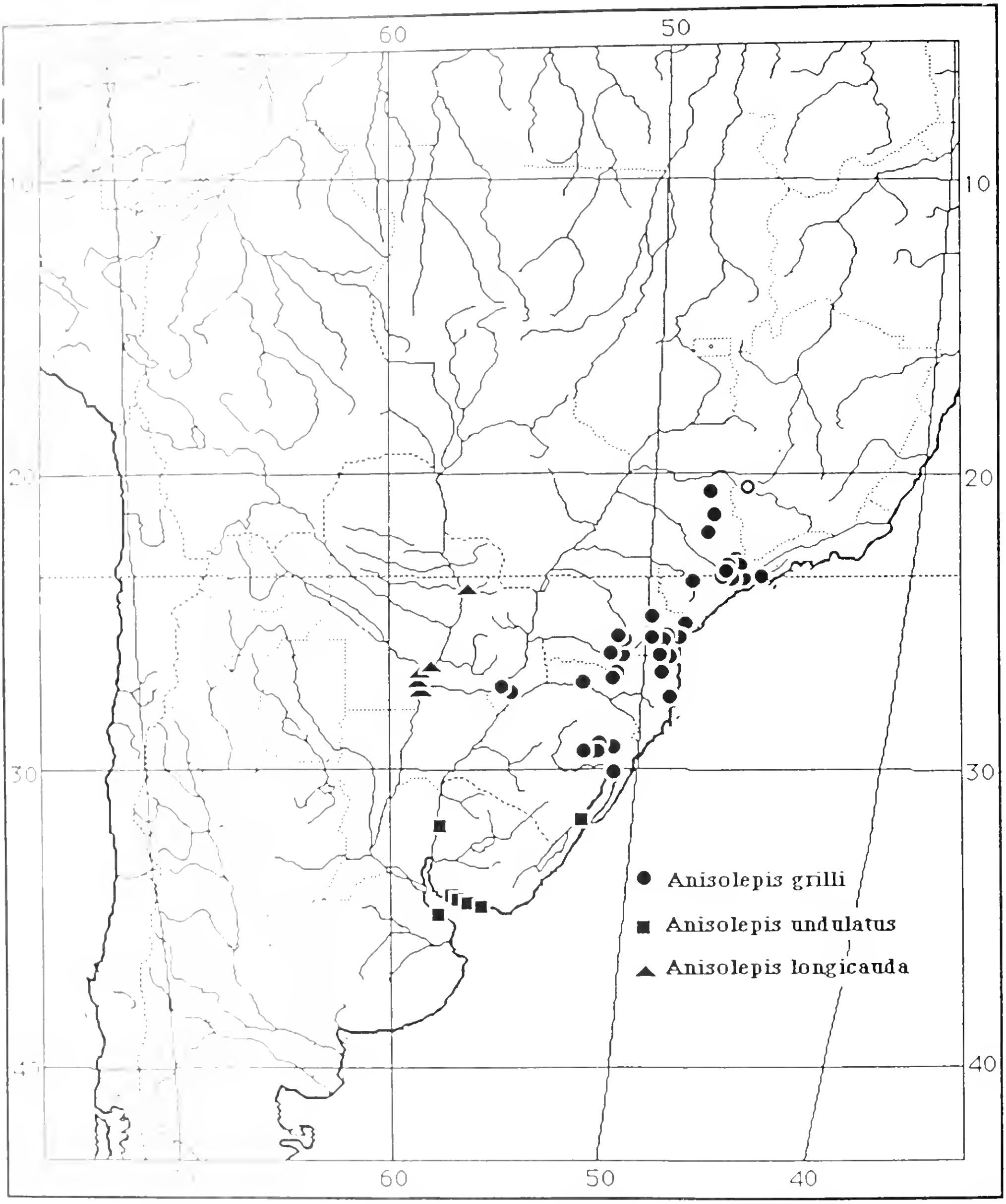
A field report on this species is that by W. W. Milstead for a specimen from Rio Grande do Sul, Brazil, misidentified by him as *A. undulatus* but confirmed by us as *A. grilli*. We have information on this specimen both from a letter from Milstead to one of us (RE) and from an oral report to Rand transcribed in the latter's notes. We quote both sources verbatim:

Rand: "Milstead reports that the only individual that he saw in the field was on the slender trunk of a spindly tree at the edge of a field in open second growth. It was head up several feet above the ground and had its tail wrapped in a long spiral around the tree."

Letter to Etheridge: "No. 429 [now FMNH 80115] W. W. Milstead, March 29, 1954, Brazil, R.G.S., Farrouphilha, 18 km south . . . in a small tree about midafternoon. This was on a hill in an area of dense vegetation consisting of pampas grass, weeds and small weed-like trees. The area was probably forest land that had been burned off in the past. Typical succession: forest–arson–cultivated field–worn out field–weeds."

A second field report is that by Gallardo (1977, p. 125, translated) for two specimens taken in the Reserva de Paranapiacaba, São Paulo, Brazil: ". . . they cling to the branches of shrubs in the forest, passing easily unnoticed, aided by their immobility and the grayish-greenish coloration, which matches the bark and lichens."

Reproduction. Rand (1982) removed clutches of fully shelled eggs from the oviducts of 9 individuals measuring 73 to 93



Map 2. The distribution of *Anisolepis*: *A. grilli* (circles), *A. undulatus* (squares), and *A. longicauda* (triangles). Solid symbols represent localities from which specimens were seen by us.

mm (M = 82.8 mm) snout–vent length. Clutch size varied from 4 to 11 (M = 8.1), egg volume from 0.4 to 0.7 ml (M = 0.6 ml) and clutch volume from 2.6 to 8.0 ml (M = 4.8 ml).

Karyotype and DNA Content. The karyotype is 2n = 36 (12 macrochromosomes + 24 microchromosomes) (Gorman, Atkins, and Holzinger, 1967; Gorman, 1973; Beçak *et al.*, 1973; Soma, Beçak, and Beçak, 1974). DNA content is reported by Soma, Beçak, and Beçak (1975) as 3.8 pi-

cograms, the lowest of the 15 thus far reported in iguanians (Olmo, 1984).

Miscellaneous. De Queiroz (1982) reported (as *A. undulatus*) the presence of 14 scleral ossicles, with numbers 1, 6, and 8 positive, and numbers 4, 7, and 10 negative, a common pattern in pleurodont iguanians. Arnold (1984) states that this species has a distinctive, swollen insertion of the *m. retractor lateralis anterior* of the hemipenis, a condition it shares with *A. longicauda*.

Discussion. Capocaccia (1961) listed two specimens of *A. grilli* in the Museo Civico di Storia Naturale di Genova, from Palmeira and Curityba (=Curitiba), Brazil, as syntypes. Through the kindness of Dr. Lilia Capocaccia we have been able to examine these specimens and find that their scale counts and other data are within the expected ranges of variation of *A. grilli*. However, the type description (Boulenger, 1891a) was based solely on the two British Museum specimens from Palmeira, and thus, under the provisions of Article 72(b) of the International Code of Zoological Nomenclature adopted in 1985, only these two specimens may be considered syntypes.

Anisolepis undulatus (Wiegmann, 1834)
Figures 7, 8, 9, and 10; Tables 1–4

1834 *L.* [*aemanctus*] *undulatus* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46.—Type locality: "Brasilia". (Holotype: Zool. Mus. Berlin No. 497).

1837 *Laemanctus ondulatus* (*lapsus*)—Duméril and Bibron, Erpét. gén., Paris, 4: 75.

1843 *Laemanctus (Urostrophus) undulatus*—Fitzinger, Syst. Rep., Wien, 1: 62.

1845 *Ecphymotes undulatus*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London, 185.

1885 *Anisolepis Iheringii* Boulenger, Ann. Mag. Nat. Hist., London, (5)16: 86.—Type locality: "Province Rio Grande do Sul . . . S. Lorenzo, on the southern border of the Lagoa dos Patos." (Syntypes: Brit. Mus. Nat. Hist. No. 85.6.26.4–5 [RR 1946.8.5.90–1].)

1885 *Anisolepis iheringii*—Boulenger, Cat. Liz. Brit. Mus., London, 2: 122; pl. 9, fig. 3.

1887 *Anisolepis undulatus*—Boulenger, Cat. Liz. Brit. Mus., London, 3: 500 (*Anisolepis iheringi* synonymized).

1895 *Anisolepis Bruchi* Koslowsky, Rev. Mus. La Plata, 6: 417; pl. 1.—Type locality: "Punta Lara," Provincia de Buenos Aires, Argentina. (Holotype Museo de La Plata, not located).

1896 *Anisolepis undulatus*—Werner, Verhandl. Zool. Bot. Ges. Wien, 46: 471. (*Anisolepis bruchi* synonymized).

1960 *Anisolepis undulatus*—Vaz-Ferreira and Sierra de Soriano, Rev. Fac. Human. Cienc., 18: 20.

Diagnosis. A. undulatus differs from *A. grilli* and *A. longicauda* in having a more distinctively heterogeneous scalation: dorsal body scales abruptly larger than, rather than grading into lateral body scales, nape with enlarged erect scales, and a conspicuous dorsolateral row of large, keeled scales. It further differs from *A. grilli* in having uni- or multicarinate supradigital scales on the hand, the keeled ventral body scales in 13 to 19 rather than 17 to 25 rows, and a smaller maximum adult size (females 83 mm, males 70 mm, versus females 97 mm, males 79 mm). It further differs from *A. longicauda* in having an external ear opening larger than, rather than conspicuously smaller than, the interparietal scale, an antehumeral-transverse gular fold, and a shorter tail (mean tail/total in males 73, females 71, versus males 77, females 74).

Etymology. Named *undulatus* because of the zig-zag dorsal pattern.

Description. Head (Fig. 9). Head scales small, more or less swollen, smooth or bluntly keeled. Rostral subpentagonal, two to three times as wide as high. Five postrostrals. Nasal oval or round, nostril central or slightly posterior in position, in contact with the first supralabial, separated from the rostral by 1 postrostral. Five to 7 scales between the nasals dorsally. Frontonasal scales smooth, convex, relatively uniform in size. Six to 11 scales between the posterior canthals. Supraorbital semicircles separated by 1, rarely in contact or separated by 2 scale rows. Supraoculars enlarged medially, transverse or not, completely or incompletely separated from the semicircles by a circumorbital series. Scales of the interparietal region usually largest laterally, about the same size or some of them a little smaller than those of the frontonasal region. Interparietal larger than surrounding scales, oval, separated from

the semicircles by 1 to 2 scales on each side, from the nape granules by 4 to 8 scales of varying size. Canthals 2 to 4, the anteriormost oriented above the nasal and separated from the nasal by 1 scale, 1 or more granules, or in contact. Superciliaries 7 to 8, the first 2 or 3 elongate and strongly and obliquely overlapping posteriorly. The posterior superciliaries less elongate and tending to overlap anteriorly. One to 2 preoculars (usually 1), in contact with the posterior canthal or separated by a polygonal scale. One subocular. Postoculars not well differentiated. Loreals 11 to 26, varying very much in shape and size. A single row of lorilabials, extending anteriorly below the nasal, posteriorly between subocular and supralabials. (Rarely the subocular may be in contact with supralabials.) Supralabials 7 to 9, the sixth or seventh below the center of the eye.

Temporals small, rather uniform in size, smooth or weakly keeled, 8 to 12 between orbit and ear. An indistinct zone of larger scales separating upper and lower temporals. Anterior auriculars like lower temporals, not enlarged, but anterior margin of ear "beaded." Posterior auriculars granular. Ear round or vertically oval, not or not much larger than interparietal.

Mental subpentagonal, wider than high, in contact with 2 postmentals (=first sublabials) between the infralabials. Three to 5 sublabials in sequence with the first sublabial on each side. Only the first sublabials in contact with the infralabials. Eight to 10 infralabials, smaller than or only equal to the scales of the sublabial series. Central gulars smooth or keeled, sometimes swollen, juxtaposed, subimbricate or imbricate, becoming larger, pointed and very distinctly keeled and imbricate at the transverse gular fold (Fig. 10), which is continued laterally on the two sides as antehumeral folds. Pregular fold well defined or indistinct.

Body. A middorsal zone 6 to 9 rows wide, with enlarged keeled imbricate scales, the 2 largest rows separated by 2 to 3 rows of irregularly smaller keeled imbricate scales, the scales anteriorly smaller and more pointed, posteriorly becoming larger and truncate. On the nape, erect middorsal scales behind the pileus grading into the much larger keeled, imbricate, often truncate scales of the middorsal zone. Laterally on the nape, often 2 rows of distinctly enlarged spinose scales, interrupted or not, 1, less frequent, beginning at the intertemporal area and continuing as swollen keeled scales above the ear to beyond the shoulder, the second, invariably present and almost always continuous, starting from the posterior lower corner of the ear, and perhaps tapering posteriorly, ending at the shoulder.

On the flanks, usually an area of smaller swollen keeled scales, very unequal in size, separating the middorsal zone from a dorsolateral line of 1 to 4 rows of enlarged keeled scales that continues forward, sometimes interrupted, to join the upper line of enlarged scales. Below this upper line of enlarged flank scales, if present, an area of mostly smaller swollen keeled scales but with irregular broken rows of larger scales. Still below this and 5 rows above the ventrals a single, usually regular, but sometimes interrupted, line of enlarged scales from the thigh to the zone of granular smooth scales that lies behind the shoulder and in the axilla.

Ventrals much larger, strongly keeled, mucronate or notched, the keels in line, in 13 to 19 longitudinal rows.

Limbs. Brachials: suprabrachials and prebrachials keeled, imbricate except at immediate insertion of arm. Infra- and postbrachials granular, swollen. Antebrachials: keeled and imbricate all around. Carpals: supracarpals keeled, imbricate. Infracarpals smooth, imbricate. Digitals of hand: supradigitals uni- or multicarinate, imbricate, wider than long, truncate or notched. Infradigitals smooth, imbricate. Axilla granular.

Femorals: supra-, pre-, and infrafemorals keeled, imbricate, truncate, as large as middorsals. Postfemorals granular. Scales at knee smaller. Tibials: keeled, imbricate

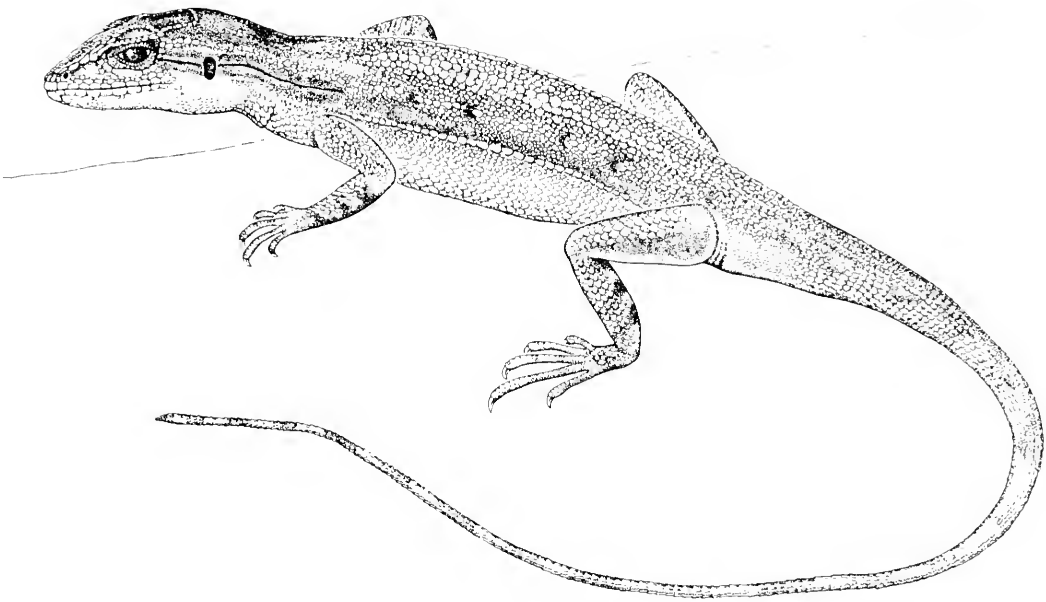


Figure 7. *Anisolepis undulatus*, USNM 65545, 75 mm snout–vent, adult female from Paysandú, Uruguay.

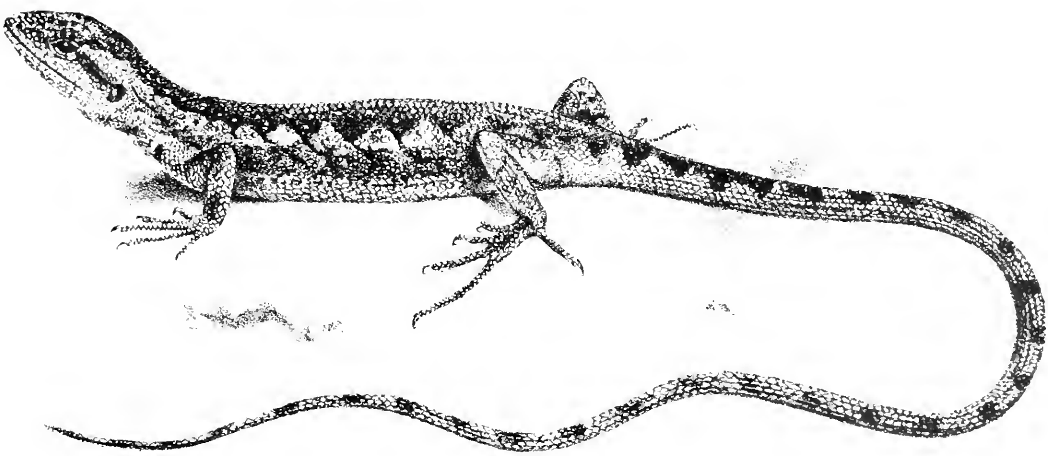


Figure 8. *Anisolepis undulatus*, reproduced from Boulenger (1885c), 2: pl. 9, fig. 3 (as *Anisolepis iheringi*).

all around, smaller than middorsals. A granular zone at the ankle dorsally. Tarsals: supratarsals keeled, imbricate. Infratarsals smooth, imbricate, swollen. Digitals of foot: supradigitals keeled, imbricate, truncate, as long as wide. Infradigitals smooth, as wide as or wider than long. Groin granular. Axillary pit shallow or absent. No inguinal pit.

Tail. Dorsum of base of tail like middorsal zone. Distally all scales nearly equal in size and all keeled.

The scalation pattern of *Anisolepis undulatus* is very similar to that of certain species of the North American phrynosomatid (*sensu* Frost and Etheridge, 1989) genus *Urosaurus*, e.g., *U. ornatus* (Mittleman, 1942, see especially fig. 3), in that large, keeled paravertebral scales are medially separated by smaller scales, and abruptly larger than adjacent flank scales, the flank scales with rows or patches of larger scales.

Color and Pattern. (Figs. 7 and 8). There appear to be two major color patterns—one that was figured by Boulenger (1885c) for the type of *A. iheringi*, another corresponding to Koslowsky's (1895) figure of *Anisolepis bruchi*. The first ("zig-zag" or "undulate") pattern, which is quite like that of many specimens of *A. grilli*, has been well described by Boulenger: "Olive brown, with a series of triangular dark brown spots on each side of the vertebral line, forming a zig-zag band; this is bordered externally with yellowish or reddish; the triangular spots may send forth narrow dark brown lines obliquely directed posteriorly down the sides; lower surfaces yellowish or coppery, the throat with a few blackish dots or longitudinal lines; tail above with a series of rhomboidal dark, light-edged spots."

The second ("lineate") pattern we describe from a Uruguayan specimen (DZVU 280, from near Carrasco, Canelones District, near Montevideo): Head above dark brown. On each side a light grayish band from the upper posterior border of the orbit extending backward above the ear onto the dorsum. Light brown on upper labials broadening backwards to encompass the lower two-thirds of the ear, narrowing again to a grayish line ending posteriorly in front of shoulder. Body with a wide middorsal brown stripe continuous forward with brown of the head, on the body narrowly bordered on each side by a slightly undulating line of darker brown that also serves as the upper margin of a dorsolateral light line continuous with that on the nape. Below this light stripe a wide zone of dark brown on the flank bounded near the ventrals by a narrow ventrolateral grayish streak restricted to the single line of enlarged scales ventrolaterally on the lower flanks. The remaining lower flank scales light purplish brown like the adjoining ventrals. Belly without spots or streaks, lighter anteriorly, darker posteriorly. Throat darker than anterior belly, purplish brown. Limbs below light like anterior belly. Tail above like dorsum at base but dorsolateral lines fading into the light, slightly smudged color of the sides of the tail. Tail below more smudged and mottled than the side of the tail but ground color light.

Distribution. (Map 2). In Brazil *A. undulatus* is known with certainty only from the type locality, São Lourenço do Sul on the western border of Lagoa dos Patos in eastern Rio Grande do Sul. In Uruguay it is known from Paysandú, on the Río Uruguay, and along the northern shore of the Rio de La Plata in the departments of Canelones and San José, and in Argentina from Punta Lara, Buenos Aires Province, just across the bay from Montevideo. Gallardo (1977) commented that the species was uncommon and had not been retaken in Punta Lara at his date of writing, and the more recent attempts (J. Williams, 1984, 1985, in litt.) to rediscover this species at the same locality have been unsuccessful. The specimen reported as *Anisolepis undulatus* from Santa Fé, Argentina, by Günther (1897) is an *A. longicauda* (BMNH 98.11.3.1), now a skeleton.

Behavior. Gallardo (1980, p. 334) states in a general review of the ecology of the

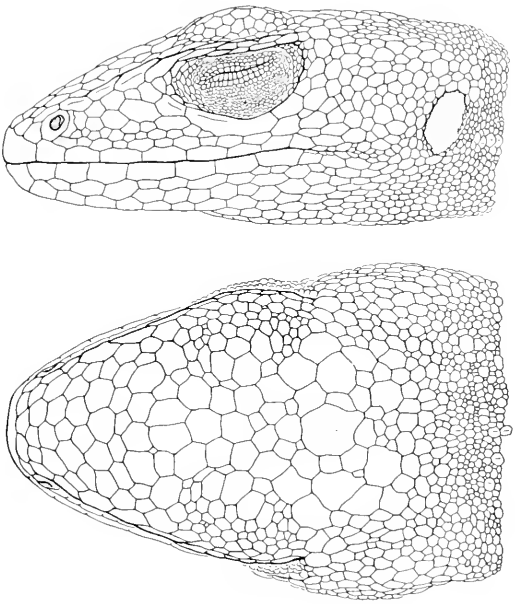


Figure 9. Head scales of *Anisolepis undulatus*, MCZ 84031 from Rio Grande do Sul, Brazil: Top, left lateral. Bottom, dorsal.

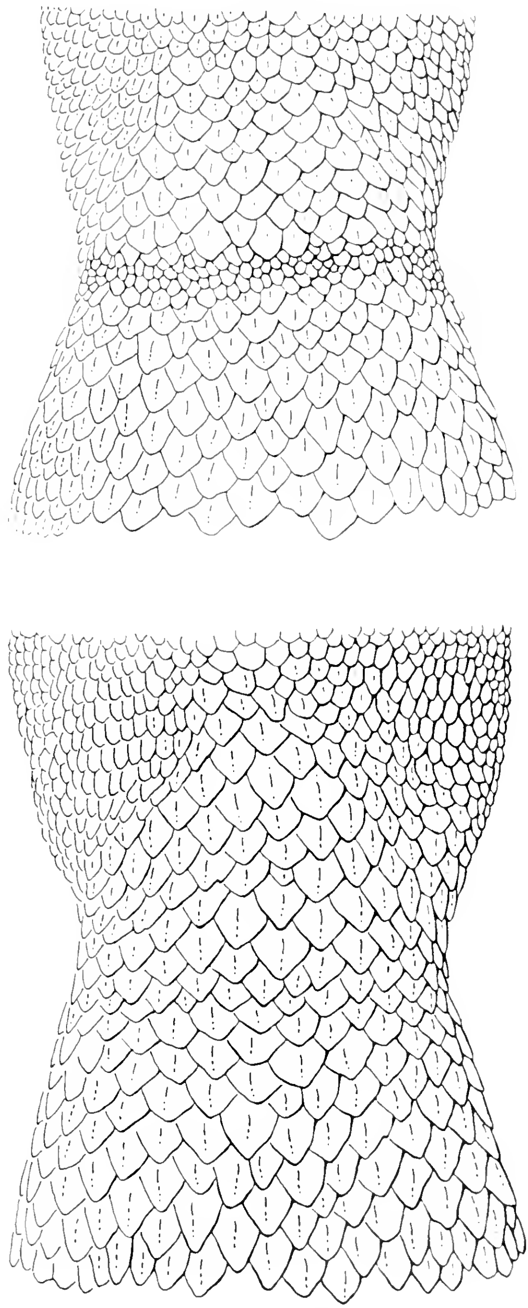


Figure 10. Ventral view of the posterior throat and anterior body region illustrating the presence of a transverse gular fold in (Top) *Anisolepis undulatus*, MCZ 84031 from Rio Grande do Sul, Brazil, and its absence in (Bottom) *Anisolepis longicauda*, MCZ 147353, syntype from mouth of the Río del Oro, Chaco, Argentina.

herpetofauna of Buenos Aires Province that this species climbs on the trunks of trees and bushes, but he does not say that this is his personal observation. He may have inferred the habitat and behavior of this species from that of the related species *A. grilli*, which he had seen in Brazil (see above).

Reproduction. Rand (1982) found four eggs in an individual 63 mm snout–vent length. Each egg had a volume of 0.5 ml, and the entire clutch a volume of 2.0 ml.

Miscellaneous. Zug (1971) reports the following characteristics of the arterial system: the sternohyoid and external carotids are separate but continuous; there is a short common subclavian trunk; the origins of the subclavians and dorsal aorta are clearly separated and lie beneath the heart; the celiac artery arises anterior to and well separated from the mesenterics; and the mesenterics arise as a common trunk.

Discussion. Werner (1896) listed *A. bruchi* as a synonym of *A. undulatus*, but in his discussion he compared *undulatus* only

with *grilli*. Berg (1898) accepted the synonomy without comment. Our own examinations leave the status of *bruchi* in doubt. In Brazil, where *Anisolepis undulatus* is known with certainty only from the type locality, the pattern is like that illustrated by Boulenger (1885c), and females (N = 24) range in size from 54 to 74 mm. We have seen only three males and five females from Uruguay. All of them have the pattern illustrated for *bruchi* by Koslowsky (1895), and the females range in snout–vent length from 75 to 88 mm. On scale counts and proportions, however, Brazilian and Uruguayan specimens are indistinguishable. Here we adopt a conservative position and leave *bruchi* in the synonymy of *A. undulatus*.

Anisolepis longicauda (Boulenger, 1891) new combination
Figures 10, 11, and 12; Tables 1–4

1891 *Aptycholaemus longicauda* Boulenger, Ann. Mag. Nat. Hist., London, (6)8: 85.—Type locality: "Riacho del Oro, Argentina" = mouth of the Río del Oro into the Río Paraguay. (Syntypes: Brit. Mus. Nat. Hist. No. 91.6.17.1; Zool. Mus. Køb., 2 unnumbered; Mus. Comp. Zool. No. 147353.)

1895 *Anisolepis argentinus* Koslowsky, Rev. Mus. La Plata, 6: 419; pl. 2.—Type locality: "Sierra de la Ventana, cerca de Bahía Blanca".—Corrected type locality (Koslowsky, 1898): "el territorio de Misiones." (Holotype: ? Museo de La Plata, not located.)

1897 *Anisolepis undulatus*—Günther, Ann. Mag. Nat. Hist., London, 20(6): 365.

1898 *Anisolepis argentinus*—Koslowsky, Rev. Mus. La Plata, 8: 167.

1898 *Aptycholaemus longicauda*—Berg, Ann. Mus. Buenos Aires, 6: 4 (*Anisolepis argentinus* synonymized.)

Diagnosis. A. longicauda differs from *A. undulatus* and *A. grilli* in lacking an antehumeral-transverse gular fold, in having an external ear opening conspicuously smaller, rather than larger, than the interparietal scale, and a longer tail (mean tail/total length 0.77 in males, 0.74 in females). It further differs from *A. undulatus* in having less distinctively heterogeneous scalation: enlarged dorsal body scales grading into rather than abruptly distinct from lateral body scales, nape without enlarged, projecting scales, no dorsolateral row of large, keeled scales, and a larger maximum size (snout–vent length in males 79 mm, females 98 mm, versus males 70 mm, females 83 mm). It further differs from *A. grilli* in having multicarinate rather than smooth supradigital scales.

Etymology. So named because of the long tail.

Description. Head (Fig. 11). Head scales small, smooth, flat. Rostral subhexagonal, more than two times as wide as long. Five postrostrals. Nasal flask-shaped, nostril posterodorsal in position, separated from the rostral by 1 scale and from the first supralabial by a smaller one or narrowly in contact. Five to 6 small, smooth, polygonal scales between the nasals dorsally. Frontonasal scales smooth, flat, polygonal, irregular in size. Five to 8 scales across snout at posterior canthals. Supraorbital semicircles separated medially by 1 to 3 rows. Supraoculars little differentiated, the centromedial scales a little enlarged, 4 to 5 scales across supraocular area. A circumorbital series separating supraoculars from semicircles.

Scales of the interparietal region small, smooth, flat, irregular in size. Interparietal larger than surrounding scales, subpentagonal, separated from the semicircles by 2 scales on each side and from the nape granules by 6 to 7 scales grading in size posteriorly. Canthals 4, the anteriormost above and in contact with the nasal. Superciliaries 7 to 8, the first largest and longest, distinctly oblique, the next 3 or 4 still elongate and with slightly oblique sutures, the remaining rectangular. One to 2 preoculars, in contact with the first canthal or separated by 1 scale. One subocular. Postoculars 2 or 4, not sharply differentiated from temporals. Loreals 18 to 25, grading from large posteriorly to small anteriorly. A single row of more or less elongate lorilabials extending anteriorly below the nasal and backward to separate the subocular from the supralabials. Supralabials 9 (the eighth below the center of the eye).

Lower temporals small, smooth, flat, 11 to 14 between orbit and ear. A rather dis-

tinct double intertemporal line of enlarged scales separating upper and lower temporals. Anterior auriculars not distinct from temporals, margin weakly beaded. Posterior auriculars granular. Ear small, oblique, somewhat or much smaller than interparietal.

Mental pentagonal, in contact with 2 postmentals (=first sublabials), as long as or longer than wide, between infralabials. Three to 6 sublabials in sequence with the first sublabial of each side. Only the first sublabial on each side in contact with the infralabials. Infralabials 9, all deeper, hence larger than the supralabials.

Central gulars small, smooth, juxtaposed, grading into larger imbricate keeled scales that join the ventrals without any intervening granular zone (Fig. 10). No antehumeral-transverse gular fold.

Body. A dorsal zone of distinctly enlarged subimbricate scales (11 to 12 rows) tending to be largest middorsally, all keeled. Nape scales subimbricate, granular, irregular in size, grading above the shoulder into the keeled scales of the dorsal zone. No enlarged rows on nape. Flank scales below the dorsal zone smaller, subimbricate, still keeled but more frequently elongate, irregular in size. Near the ventrals an interrupted line of imbricate keeled scales, again irregular in size.

Ventrals much larger, strongly keeled, imbricate, mucronate, in 15 to 19 transverse rows, keels in line. Scales at the anterior margin of the vent tending to be transverse, smooth in a single row and much smaller than the ventrals. Vestiges of a lower lateral line of enlarged scales present or absent. Anterior to the vent, three rows of keeled scales much smaller than the ventrals, but much larger than the immediately preanal scales.

Limbs. Brachials: suprabrachials and prebrachials keeled, imbricate except at immediate insertion of arm. Infrabrachials keeled but smaller than suprabrachials. Postbrachials subgranular. Anterior brachials: keeled and imbricate all around, smaller at elbow. Carpals: supracarpals keeled, imbricate. Infracarpals smooth, imbricate. Digitals of hand: supradigitals multicarinate, imbricate, truncate, very little wider than long. Infradigitals smooth, imbricate, a little wider than long proximally, narrower distally.

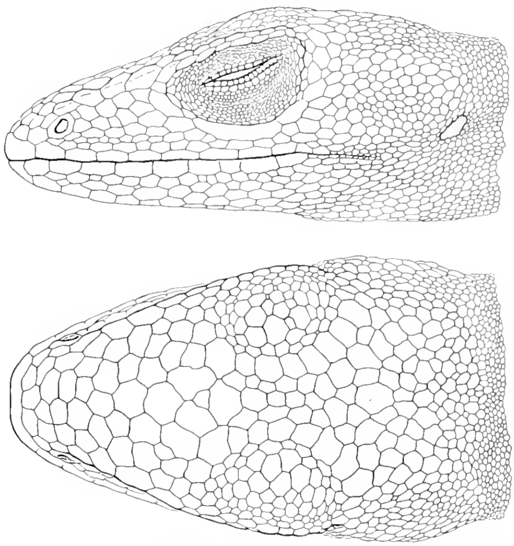


Figure 11. Head scales of *Anisolepis longicauda*, MCZ 147353, syntype from mouth of Río del Oro, Chaco, Argentina: Top, left lateral. Bottom, dorsal.

Femorals: supra-, pre-, and postfemorals imbricate, keeled, truncate, as large as middorsals. Infrafemorals granular. Scales at knee smaller. Tibials: keeled, imbricate all round except granular at ankle, smaller than middorsals. Tarsals: supratarsals keeled, imbricate. Infratarsals smooth, imbricate. Digitals of foot: supradigitals multicarinate, imbricate, truncate. Infradigitals smooth, imbricate, wider than long only at digital joints. Lamellae under fourth toe 20 to 29. Groin granular. No axillary pit. No inguinal pit.

Tail. Compressed. Scales of dorsum of tail in size and keeling like middorsal zone. Scales of base of tail immediately behind vent granular. Distally all scales keeled, somewhat larger than middorsals, subequal.

Color and Pattern. (Fig. 12). The syntypes now are faded, and color freshly preserved has been described only by Boulenger (1891b) and Koslowsky (1895). The

two descriptions are quite parallel, and the briefer description of Boulenger will serve: "Pale brown above, with darker broad dorsal stripe, which may be edged on each side by a fine blackish line; a blackish streak on the canthus rostralis, and a black-edged streak from the eye to the neck passing through the tympanum; upper lips and lower parts cream-colored."

Distribution. (Map 2). In northern Argentina, *A. longicauda* known from several localities near the west bank of the Río Paraguay in eastern Chaco Province, and from unspecified localities in Santa Fé and Misiones Provinces. In Paraguay, it is known only from San Pedro on the east bank of the Río Paraguay, and from an unspecified locality.

Behavior. For ecology and behavior there are no reports at all. In *Anolis* the conjoined features of a dorsal zone of enlarged keeled scales, keeled ventrals, and a pattern of light lines on the lower flanks occur in those anoles adapted to life on bushes and grasses (e.g., *Anolis notopholis*, *A. auratus*), and in the grass-bush anoles of Hispaniola and Puerto Rico (Williams, 1983) or in semiaquatic anoles such as the *lionotus* group of Central America and northwest South America, the latter found only at the borders of streams or the rocks within them (Williams, 1984). In neither ecological situation are the patterns of scales and color quite consistent, only very usual. From the descriptions and pictures of the habitats of *Anisolepis longicauda* and *A. undulatus* that have been made available to us, it seems probable that these are typically inhabitants of bushes and tall grasses, particularly in areas (*esteros* or *bañados*) that are seasonally flooded. (See also our remarks under *A. undulatus* comparing that species with *Urosaurus*.)

Miscellaneous. The thyroid gland is reported to have two well-defined lobes connected by a narrow isthmus (Lynn, O'Brien, and Herhenreader, 1966). Underwood (1970) reported 13 scleral ossicles, numbers 1, 6, and 8 plus, and 4, 7, and 9 minus the most common number [illegible] and in pleurodont iguanians. Arnold (1984) states that this species has a distinctive, swollen insertion of the *m. retractor lateralis anterior*, a condition it shares with *A. grilli*.

RELATIONSHIPS (R. Etheridge)

The para-anoles were first so-called by Williams and me during the course of informal discussions of anole relationships when it appeared to us that the presence of a spinulate scale surface, with elongate spinules on the scale organs and elongate and differentiated spinules on the subdigital surface implied a close relationship between these five species and the vast radiation of anoles. Except for their loss of caudal autotomy and a middorsal scale row it seemed to us at the time that para-anoles were almost ideal ancestors of anoles. I have today all but abandoned (Williams has quite abandoned) that assessment, having learned much more about other components of what has recently been formally recognized as the iguanian family Polychridae (Frost and Etheridge, 1989). The relationship implied by the term "para-anole" may well be misleading. Here follows the history of my thoughts and the thoughts of others on the questions of para-anole relationships.

Boulenger (1885b) was first to note the similarities of para-anoles in his description of *Anisolepis*, noting that it is "allied to *Enyalius*, *Urostrophus*, and *Leiosaurus*, which have likewise smooth infradigital lamellae, no femoral pores, and, like *Polychrus* and the Gekkonidae, abdominal ribs and no fontanelle in the sternum," and in his description of *Aptycholaemus* (Boulenger, 1891b), in which he said that it is allied to *Urostrophus* and *Anisolepis*, "but differs from both in the absence of a gular fold and dorsal lepidosis." In his Catalogue, Boulenger (1885c) also transferred the Chilean lizard described as *Leiosaurus torquatus* (Philippi, *in* Philippi and Landbeck, 1861) to the genus *Urostrophus*. This was the first suggestion of possible close relationship between *Pristidactylus* and *Urostrophus*.

In a thesis on the osteology and rela-

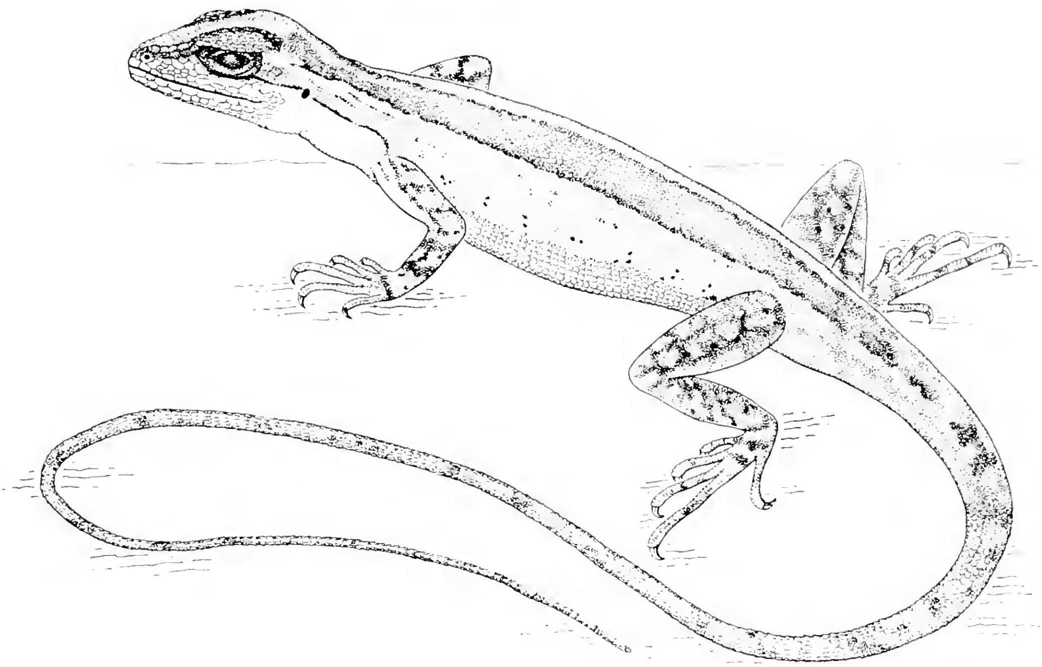


Figure 12. *Anisolepis longicauda*, Nat. Mus. Wien No. 12971, female, snout–vent length 90 mm, from Paraguay.

tionships of anoles (*Chamaeolis*, *Phenacosaurus*, *Chamaelinorops*, *Anolis*), I compared anoles with *Polychrus* and *Aptycholaemus* (Etheridge, 1960, table vii). The data on *Aptycholaemus* was based upon a misidentified specimen of *Anisolepis grilli*. The suggestion was made that "*Polychrus* shows the closest affinities with the anole group," and although insufficient data were available to form a proper evaluation of the position of *Anisolepis* (i.e., *Aptycholaemus* of the thesis), it was said of the latter that "with respect to the anoles, correspondence in characters was very nearly as close as that between *Polychrus* and the anoles."

In a review of the genus *Enyalius*, Etheridge (1969) concluded that "*Anisolepis* and *Aptycholaemus* are indeed very similar to each other, and of iguanids are most like *Enyalius*" and that "the differences that separate *Anisolepis* and *Aptycholaemus*, considering the two together, from *Enyalius* are few and relatively trivial," and also remarked that "*Enyalius bilineatus* is in some respects transitional between *Anisolepis* and *Aptycholaemus* on the one hand and the remaining species of *Enyalius* on the other."

Recently Etheridge and Williams (1985) reviewed the confusion in allocation to *Urostrophus* of species now referred to *Pristidactylus scapulatus* and *Pristidactylus torquatus*. Following the then unpublished work of Etheridge and de Queiroz (1988), we considered the genera *Pristidactylus*, *Leiosaurus* (including *Aperopristis*), *Diplolaemus*, and *Enyalius* to form a monophyletic group called the "leiosaurs."

Williams (1988) accepted the monophyly of anoloids, but in a footnote he included the para-anoles within the leiosaurs without further comment. Most of his discussion is irrelevant to present issues. However, relevant to the present work is his suggestion that anoles and *Polychrus* are sister taxa.

Thus, directly or indirectly, the para-anoles have been closely linked to one another as a group, and to *Polychrus*, the anoles and the leiosaurs, all of which, collectively, form the family Polychridae of Frost and Etheridge (1989).

In their formal, cladistic analysis of "Iguanidae," Etheridge and de Queiroz (1988) found no evidence for monophyly of the family, but eight monophyletic, suprageneric groups were recognized. One of these, the anoloids, contained the para-anoles together with *Polychrus*, *Enyalius*, *Pristidactylus*, *Diplolaemus*, *Anolis*, *Chamaeolis*, *Chamaelinorops*, and *Phenacosaurus*. Anoloids were specified by numerous synapomorphies, including the uniquely derived nuchal endolymphatic sacs. Thus, the para-anoles, together with all of the genera (and only those genera) to which they have been said, directly or indirectly, to be related, formed a single monophyletic group.

Polychrus was recognized as the sister taxon to all of the remaining anoloids, called the "spinulate anoloids," the latter specified by the loss of femoral pores, elongation of the dentary, and the acquisition of a spinulate oberhautchen with the spinules of the scale organs and subdigital scales longer than the background spinules. Three groups of spinulate anoloids were recognized: leiosaurs (*Enyalius*, *Pristidactylus*, *Diploaemus*, *Leiosaurus*, incl. *Aperopristis*), para-anoles (*Urostrophus*, *Anisolepis*, *Aptycholaemus*), and anoles (*Chamaeolis*, *Anolis*, *Chamaelinorops*, *Phenacosaurus*). Monophyly of both the leiosaurs and anoles was thought to be well supported, the former by presence of the uniquely derived divided distal subdigital scales and other derived features, the latter by the acquisition of an extensile gular fan with elongate second ceratobranchials, a distinctive digital pad, scale organs with elongate filaments, and other synapomorphies. Eight synapomorphies were provided for para-anoles: 1) lateral margins of the clavicles become angular and hooked, 2) a very small secondary coracoid fenestra was acquired, 3) sternal ribs have been reduced from four pairs to three, 4) caudal autotomy was lost, 5) scale organ spinules attained a height of at least five microns, 6) subdigital spinules became differentiated, with seta-prongs present, 7) a mid-dorsal scale row has been lost, and 8) sexual dichromatism has been lost. However, Etheridge and de Queiroz were more tentative in their recognition of para-anoles as a monophyletic assemblage, pointing out that characters 1 and 2 (above) are possible synapomorphies for leiosaurs plus para-anoles, characters 3, 5, and 6 possible synapomorphies for anoles and para-anoles, and that the remaining transformations have occurred numerous times within the family. Figure 13a illustrates the relationships of the anoloids proposed by Etheridge and de Queiroz (1988), adapted from their figure 9 to facilitate comparison with the work of Frost and Etheridge (1989) discussed below.

No synapomorphies uniting *Urostrophus vautieri* with *U. gallardoi* were discovered; thus, *Urostrophus* was considered paraphyletic with respect to *Anisolepis* and *Aptycholaemus*. The latter genera were said to share a reduction in the secondary cusps of the marginal tooth crowns, loss of the posterolateral processes of the basisphenoid, and the acquisition of a ventrolateral row of enlarged scales and ventral body scales with sharp keels in parallel rows. *Aptycholaemus* was diagnosed by loss of the transverse gular fold, elongation of the tail, and reduction of the external ear, but in the absence of synapomorphies that would unite *Anisolepis undulatus* with *A. grilli*, the genus *Anisolepis* was considered paraphyletic.

The most recent work on the possible affinities of para-anoles is contained in Frost and Etheridge's (1989) phylogenetic analysis of the Iguania. The anoloids of Etheridge and de Queiroz (1988) were discovered to form a monophyletic group in all obtained trees, and the group was formally proposed as the iguanian family Polychridae Fitzinger 1843. Monophyly of

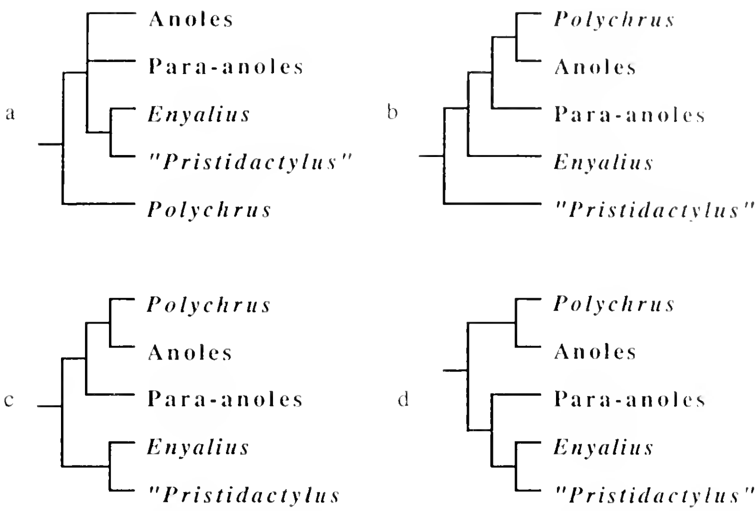


Figure 13. Four possible patterns of relationships of para-anoles to other polychrid iguanians: a) according to Etheridge and de Queiroz (1988); b), c), and d) according to Frost and Etheridge (1989).

the family was supported by endolymphatic sacs that penetrate the nuchal musculature, and strongly bicapitate, bisulcate hemipenes (unicapitate in some *Anolis*, presumably reversed). Five polychrid terminal taxa were employed: *Polychrus*, the anoles, the para-anoles (i.e., *Urostrophus* and *Anisolepis*; *Aptycholaemus* was synonymized with *Anisolepis* based on our unpublished manuscript of the present work), *Enyalius*, and "*Pristidactylus*," the latter considered to be paraphyletic with respect to *Diplolaemus* and *Leiosaurus* (including *Aperopristis*) and thus placed in quotes. Following Etheridge and de Queiroz (1988), *Urostrophus* was considered to be a metataxon, i.e., a supraspecific taxon for which evidence for monophyly is either lacking or ambiguous. Three equally parsimonious tree topologies were discovered for the relationships of these five terminal taxa (Figs. 13b, c, and d). In all three, *Polychrus* and the anoles were sister taxa, corroborated by four unambiguously placed characters: long second ceratobranchials, anterior elongation of the sternum (incorrectly stated as anterior process of interclavicle by Frost and Etheridge, 1989, p. 22), loss of cervical ribs on vertebra four, and loss of a gular fold. In two trees, para-anoles were the sister taxon of *Polychrus* + anoles (Figs. 13b and c), supported by the following characters: three (or fewer) sternal ribs, loss of caudal autotomy (reversed in some *Anolis*), and, ambiguously, acquisition of anole-type caudal vertebrae, difficult to evaluate in para-anoles and *Polychrus*. In one tree topology (Fig. 13d) para-anoles were the sister taxon of *Enyalius* + "*Pristidactylus*," supported by the presence of a small posterior coracoid fenestra. Thus a strict consensus tree (*sensu* Nelson, 1979) showed the para-anoles in an unresolved polytomy with *Enyalius*, "*Pristidactylus*," and the anoles + *Polychrus*. Additionally, although para-anoles were treated as a terminal taxon, they were not united by any apomorphies whose placement was independent of the network, so that their monophyly was not supported unambiguously, i.e., *Urostrophus* and *Anisolepis* may be more closely related to other polychrid genera than to each other.

In summary, the analyses of Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) provide a strong consensus that Polychridae is a monophyletic family

and that the genera *Urostrophus* and *Anisolepis* (the latter understood to include *Aptycholaemus*) are among its member genera. Further, the genus *Polychrus* and the anoles each possess a number of striking synapomorphies that strongly support their separate monophyly, but evidence for the monophyly of the leiosaurs or for the para-anoles is ambiguous. Yet to be resolved are questions of the historical relationships of these groups to one another: whether *Polychrus* is the sister taxon of all other polychrids or the sister taxon of anoles, whether para-anoles share a more recent common ancestor with anoles (and perhaps *Polychrus*), or with the leiosaurs, and whether the para-anoles themselves are monophyletic.

The polarities of a number of transformations depend on whether *Polychrus* is considered the sister taxon of anoles or of all other polychrids. The choice appears to depend on which set of homoplastic transformations is considered less likely to have occurred. If *Polychrus* is the sister taxon of other Polychridae, then homoplasy (in anoles) is indicated in: 1) elongation of second ceratobranchials, 2) loss of a transverse gular fold, 3) anterior elongation of the sternum, 4) loss of ribs on the fourth vertebra, 5) division of the mental scales, and 6) adherence of the scales above the supralabials to the underlying periosteum (the latter two characters described by Williams, 1988). If *Polychrus* is the sister taxon of the anoles, then homoplasy (in *Polychrus*) is indicated in: 1) reacquisition of subdigital keels, 2) loss of subdigital spinules, 3) loss of scale organ spinules, 4) reacquisition of femoral pores, 5) reacquisition of a short dentary, and (in anoles) 6) reacquisition of caudal autotomy.

The question of choice between a sister taxon relationship of para-anoles and anoles (with or without *Polychrus* as the latter's sister taxon) or between para-anoles and leiosaurs similarly requires a choice between conflicting sets of homoplasies. If para-anoles and anoles are sister taxa, then homoplasy is indicated (in para-anoles) in the acquisition of a small posterior coracoid fenestra and the acquisition of hook-like processes on the interclavicle. If *Polychrus* and anoles are sister taxa, then loss of caudal autotomy and of a middorsal row could be synapomorphies for *Polychrus* + anoles + para-anoles, which, in turn, would require reacquisition of autotomy within *Anolis* and of a middorsal row within *Polychrus*. However, loss of a middorsal scale row and of caudal autotomy is also characteristic of some (e.g., *Leiosaurus belli*), but not all leiosaurs, and are potential synapomorphies linking para-anoles with a specific subset of leiosaurs. If para-anoles are the sister taxon of leiosaurs, then homoplasy in para-anoles is indicated in the elongation of the subdigital spinules and in the loss of one pair of sternal ribs.

The suggestion of Etheridge and de Queiroz (1988) that *Urostrophus* may be paraphyletic rested upon the assumption that the scalation pattern common to *U. vautieri* and *U. gallardoi* is primitive, but no evidence was provided that this is the case. The *Urostrophus* pattern closely resembles that found in some *Enyalius* (e.g., *E. iheringi*) and *Pristidactylus*, while that found in *Anisolepis* closely resembles that found in other *Enyalius* (e.g., *E. bilineatus*). If, instead, the *Anisolepis* pattern is primitive (and para-anoles are, indeed, a monophyletic group), then *Urostrophus* may be considered monophyletic on the basis of a derived scale pattern.

The linking of *A. undulatus*, *A. grilli*, and *A. longicauda* to form a monophyletic group on the basis of shared derived conditions of the marginal teeth and basisphenoid (Etheridge and de Queiroz, 1988) appears to be justified. However, no derived feature has been found to be shared by *A. undulatus* and *A. grilli*, but not *A. longicauda*. Thus *Anisolepis* is a paraphyletic genus if *A. longicauda* is excluded. This conclusion is independent of the problem of polarity of scale patterns and led us to recommend in the preceding section that *Aptycholaemus* be considered a synonym of *Anisolepis*.

CONCLUSIONS

1. There is strong support for the hypothesis that: a) Polychridae is monophyletic, and b) the five species referred to *Urostrophus* and *Anisolepis* (the para-anoles) are members of that family.

2. There is strong support for the monophyletic status of *Polychrus*, the leiosaurs and the anoles, but evidence that the para-anoles form a monophyletic subset within Polychridae is not strong, and weaker still if para-anoles are nested within (rather than being a sister group of) the leiosaurs.

3. Evidence can be cited for a possible sister taxon relationship between *Polychrus* and the anoles, as well as for a sister taxon relationship between *Polychrus* and the spinulate polychrids.

4. If the para-anoles are monophyletic, and if the scalation pattern of *Urostrophus* is primitive, relative to that of *Anisolepis*, then *Urostrophus* is paraphyletic. However, monophyly of *Anisolepis* is based on other characters and is independent of whether its scalation pattern is primitive.

5. No synapomorphies united *A. undulatus* with *A. grilli* to the exclusion of *A. longicauda*. Recognition of the latter as representative of a monotypic genus by Boulenger may reflect a consideration that the absence of a transverse gular fold was a generic character. *Aptycholaemus* Boulenger 1891 is placed in the synonymy of *Anisolepis* Boulenger 1885.

6. It is clear that resolution of the relationships of the five para-anole species must await a more detailed examination of the interrelationships of Polychridae as a whole. Especially critical are questions of monophyly of the para-anoles and appropriate outgroups for polarity assessments.

A KEY TO THE SPECIES OF *UROSTROPHUS* AND *ANISOLEPIS*

1a. Ventral body scales smooth .... *Urostrophus* (2)
1b. Ventral body scales distinctly unicarinate .... *Anisolepis* (3)
2a. External ear opening large, up to three times diameter of interparietal scale; all scale counts higher (Tables 2 & 3) .... *U. gallardoi*
2b. External ear opening smaller than, equal to, or scarcely larger than interparietal scale; all scale counts lower (Tables 2 & 3) .... *U. vautieri*
3a. An antehumeral-transverse gular fold present .... (4)
3b. No antehumeral-transverse gular fold .... *A. longicauda*
4a. Dorsal body with paravertebral rows of large, keeled scales separated medially by one to three rows of smaller scales and laterally abruptly larger than adjacent flank scales; flank scales distinctly heterogeneous, with a dorsolateral series of patches of large, keeled scales and a ventrolateral row of enlarged, keeled scales, evident also on the neck .... *A. undulatus*
4b. Dorsal body scales slightly convex and keeled, grading into smaller flank scales that are smooth or weakly keeled and nowhere markedly smaller than dorsal scales; dorsolateral patches and ventrolateral rows of enlarged scales inconspicuous on the body and absent on the neck .... *A. grilli*

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LOCALITIES AND SPECIMENS EXAMINED

Museum numbers represent specimens seen by us; those represented by a skeleton or accompanied by radiographs ("x rays") are so indicated. Museum abbreviations are provided in the Acknowledgments. Specific localities are followed by degrees and minutes south latitude and west longitude.

Urostrophus gallardoi

ARGENTINA: **Córdoba:** *Dpto. Cruz del Eje:* Cruz del Eje, 300 m (30 44–64 48) BMNH 1902.5.22.4; *Dpto. Río Seco:* Sebastián Elcano (30 09–63 35), Bee de Speroni and Cabrera, 1984; *Dpto. Sobremonte:* 7 km N Puesto Nuevo (29 31–65 34) AC 070; *Dpto. Tulumba:* Isla de San Antonio (30 02–64 26) AC 159. **La Rioja:** *Dpto. Arauco:* Aimogasta (28 33–66 49) (possibly in error fide R. Laurent, in litt.) MZUSP 45908. **Misiones:** Eldorado (26 24–54 38) AC 079. **Salta:** Estancia Gutierrez (1,650 m), southern Salta, Laurent, 1985; *Dpto. Anta:* El Quebrachal (25 17–64 09) ABarrio 746; *Dpto. Orán:* Urundel (23 43–64 47) MACN 11043 (holotype of *Urostrophus gallardoi*); *Dpto. La Poma:* Quebrada Río Las Conchas (24 55–66 09) FML 01266; *Dpto. La Viña:* Río Chuña Pampa (=Chuñapampa), 10 km WNW La Viña (25 27–65 35, La Viña) FML 01296 + x ray; *Dpto. Metán:* Puesto San Borja, Sierra de Metán, 15 km W Metán (25 30–64 58) FML 00847 + x ray; *Dpto. Rosario de la Frontera:* Rosario de la Frontera (25 48–64 58) MCZ 162922, MACN 4311–24; Joachim V. Gonzalez (25 10–64 00) FML 2417–20; *Dpto. San Carlos:* 35 km N Cafayate (25 06–65 57) MCZ 162920: skeleton, MACN 12016. **Santa Fé:** No additional data: Gallardo, 1964, MACN 19740. **Santiago del Estero:** No additional data: MACN 8019–21 + x ray; *Dpto. Matará:* Campo del Cielo (27 52–61 50) Gallardo, 1964; *Dpto. Capital:* Suburbios [? de Santiago del Estero (27 47–64 16)] ABarrio 121; *Dpto. Belgrano:* Bandera (28 54–62 16) ABarrio 345. **Tucumán:** No additional data: MACN 4318–25; *Dpto. Burruyacú:* probably from 7 de Abril (26 17–64 29) or Garmendia fide R. Laurent, in litt. FML 00483.

BOLIVIA: **Santa Cruz:** Santa Cruz de la Sierra (30 44–64 48) MACN 2786–8.

Urostrophus vautieri

BRAZIL: No additional data: BMNH xxiii.3a, 57.10.28.66, 94.9.15.3: skeleton, 1913.9.30.2, ZMB 4326, 9060. **Minas Gerais:** No additional data: MCZ 5566 + x ray; Antonio Carlos (21 19–43 45) MZUSP 7068; Engenheiro Trompowski (21 18–46 17) MZUSP 4472; Lagoa Santa (19 38–43 52) Reinhardt and Lütken, 1861; Machado (21 41–45 56) MZUSP 4480, 4482, 4552–4; Poços de Caldas, 1,200 m (21 48–46 34)

MZUSP 13982; Santa Rita da Extrema (22 52–46 19) MZUSP 4477. **Paraná:** Campo do Tenente (25 59–49 41) MZUSP 36666; Curitiba (25 25–49 16) MZUSP 43010; Rio Itararé (23 10–49 42, mouth of Rio) FMNH 28863. **Rio de Janeiro:** Itatiaia (22 23–44 39) FMNH 83576, MZUSP 2273, 44681–86; Nova Friburgo (22 18–42 31) ZMB 7446(3), ZMH 02769–71 + x ray; Petrópolis (22 32–43 11) MCZ 7319, MZUSP 563, 36342; Rio [? de Janeiro], Reinhardt and Lütken, 1861; Rio de Janeiro (22 48–43 32) MNHNP 6779–80 (syntypes of *Urostrophus vautieri*); Serra de Macaé (22 10–41 50) MZUSP 418; Teresópolis (22 26–42 59) BMNH 88.9.21.1. **Rio Grande do Sul:** No additional data: BMNH 82.10.4.50–51; Passo Fundo (28 15–52 24) MZUSP 4469; Porto Alegre (30 00–51 10) ZMB 6823. **São Paulo:** Alto da Serra (=Paranapiacaba) (23 48–46 03) MZUSP 4479; Barueri (23 33–46 54) MZUSP 4473, 4481; Boraceia (23 38–45 50) MZUSP 42914–5, 45642, 49209; Botucatu (22 54–48 27) MZUSP 4467; Bragança Paulista (22 57–46 33) MZUSP 4470; Cabreúva (23 18–47 08) MZUSP 470; Caçapava (23 06–45 42) MZUSP 42699; Campo Limpo (23 12–46 48) MZUSP 11867; Campos do Jordão (22 45–45 34) MZUSP 4475, UMMZ 108632(2) + x ray; Casa Grande (23 38–45 54) MZUSP 36103; Cotia (23 37–46 56) MZUSP 8259; Faveiro (21 40–47 18) MZUSP 4483; Fazenda Barreiro Rico, Anhembi (22 48–48 08) MZUSP 7063; Fazenda Pedra Branca, Botucatu (22 52–48 26) MZUSP 29615; Garça (22 13–49 44) SDSU unnumbered; Mato Dentro, São Roque (23 42–47 08) MZUSP 10377; Mogi das Cruzes (23 31–46 11) MZUSP 999; Osasco (23 32–46 46) MZUSP 13417; Perus (23 24–46 46) MZUSP 543; Piquete (22 36–45 10) MZUSP 565, 576; Piracicaba (22 42–47 38) MZUSP 153–6, 2831–3, MCZ 133154–6; Salesópolis (23 32–45 51) MZUSP 32270, AMNH 120474; Santa Rita (21 40–47 30) Von Ihering (1899); São Paulo (22 33–46 38) FML 00830, MZUSP 2549, 3190, 4460; São Paulo: Interlagos, UMMZ 108633 + x ray; São Paulo: Represa de Santo Amaro (23 40–46 43) AMNH 120473, MZUSP 3366, 8404; São Paulo: Villa Jaguara, MZUSP 36114; Serra da Bocaina, Bananal (=Fazenda do Bonito) (22 44–44 33) MZUSP 10297; Serra Negra (22 37–46 42) MCZ 84036–7: skeleton, 84037, MZUSP 4468; São José do Barreiro, near Fazenda do Veado (22 49–44 39), Serra da Bocaina USNM 208136; São Bernardo do Campo (23 42–46 33) AMNH 120467–8; Tupi (22 45–47 32) MZUSP 4478.

PARAGUAY: No additional data: USNM 12329. PARAGUAY or ARGENTINA: ZMH 02772 + x ray.

No data: REE 2507: skeleton.

Anisolepis grilli

ARGENTINA: **La Rioja:** *Dpto. Independencia:* Patquia (30 03–66 53), Estancia Breyer (locality probably in error) USNM 73504. **Misiones:** *Dpto. Cainguás:* Dos de Mayo (27 02–54 39) MLP S.957–62; *Dpto. Guaraní:* Río Victoria (26 52–54 39, mouth of Río Victoria) MLP S.963.

BRAZIL: No additional data: ZMB 495 (type of *Laemanctus fitzingeri*), 496 (type of *Laemanctus obtusirostris*), ZMH 02764 + x ray. **Minas Gerais:** Delfinópolis (20 20–46 51) MZUSP 42688. **Paraná:** No additional data, NMW 12970 + x ray; Araucaria (25 36–49 25) MZUSP 4532–5; Curitiba, Boettger, 1905 (as *Laemanctus* tiba and Serra between Rio Negro and dCuritiba, Boettger, 1905 (as *Laemanctus undulatus*); Dorizon (25 55–50 58) MCZ 133190, MZUSP 4496–8, 6866–9, 10132–3; Morretes (25 28–48 49) MZUSP 6693; Palmeira (25 26–50 00) BMNH RR 1946.8.5.58, RR 1946.8.12.35: skeleton (syntypes of *Anisolepis grilli*); Paranaguá (25 31–48 36) REE 1952: skeleton, ZMH 02757–60 + x ray; Piraí Mirim (now Piraí do Sul) (24 31–49 57) MZUSP 6699; Porto União da Vitoria (26 15–51 05) MZUSP 4546–9: skulls; Rio Azul (25 43–50 47) MZUSP 29611; Umbará (25 53–49 19) MZUSP 8419. **Rio Grande do Sul:** Alfredo Chaves (28 57–51 33) MZUSP 4520; Carlos Barbosa (29 18–51 30) MZUSP 3726; Canela (29 22–50 50) MZUSP 4530; Farroupihlha (29 14–51 21), 18 km S, FMNH

80115; Garibaldi (29 15–51 32) MZUSP 4523; Porto Alegre (30 00–51 10) ZMB 6246. **Rio de Janeiro:** Rio de Janeiro (22 48–43 32, locality possibly in error fide P. Vanzolini, in litt.) MZUSP 463. **Santa Catarina:** No additional data: UMMZ 123813–5; Blumenau (26 55–49 04) NMW 18904 + x ray (type of *Anisolepis lionotus*); Caçador (26 47–51 00) MZUSP 4524; Ipomeia (26 57–51 06) MZUSP 4527–8; Joinville (26 18–48 50) UMMZ 122439, NMW 12969(3) + x rays; Lagoa (27 35–48 28) MCZ 133189, MZUSP 4488–92, 4499, 4501–8; Nova Teutonia (27 16–52 20) MZUSP 10344, CMNH 68364–70, UMMZ 122147, 123122–6, 123248, 123812–3; São Bento do Sul (26 15–49 22) MZUSP 4539; Valões (now Ireneópolis) (26 12–50 48) MZUSP 4545. **São Paulo:** No additional data: UMMZ 138813–4, ZMH 02761, Boettger, 1882 (as *Laemanctus undulatus*); Alto da Serra (now Paranapiacaba) (23 48–46 03) MZUSP 545, Gallardo, 1977; Alto Pimenta (now Bento de Abreu) (21 17–50 48) MZUSP 4537; Américo Brasiliense (21 43–48 07) MZUSP 4544; Baruerí (23 33–46 54) MZUSP 4511, Belém (now Francisco Morato) (23 16–46 45) MZUSP 4513; Caieiras (23 21–46 45) MZUSP 4500; Campinas (22 53–47 04) MZUSP 4525; Campo Largo (23 11–46 42) MZUSP 4536; Campo Limpo (23 12–46 48) MZUSP 4509–10, 42738, 54752; Cotia (23 37–46 53) MZUSP 4514; Estrada de Poá (23 32–46 22) MZUSP 44692; Ferraz de Vasconcelos (23 33–46 22) MZUSP 44690; Ibaté (21 57–48 00) MZUSP 36111; Ibiúna (23 34–47 13) MZUSP 42700; Itaquaciara (23 47–46 51) MZUSP 4529; Itatuba (22 28–47 38) MZUSP 42747; Jandira (23 31–46 54) MZUSP 4540, 4542; Osasco (23 32–46 46) MZUSP 2679, 7064; Pirituba (23 30–46 44) MZUSP 8392; Santa Rita (21 40–47 30) Von Ihering (1899); São Bernardo do Campo (23 42–46 33) AMNH 120467–8, MCZ 96031, 133199: skeleton, MZUSP 773, 10139–54, 11872–3, 13908, BMNH 1977.2274–6, UMMZ 138813–4; São Paulo (23 33–46 38) MZUSP 167–9, 263, 286, 540, 542, 555, 560, 561, 569, 809, 842, 2307–8, 2798–9, 3269, 3473, 4494–5, 4512, 4519, 4551, 8276, 8278, 8438, 11461, 29719, 45782: skull; São Paulo: Butantan, MZUSP 4515–8, CMNH 65044; São Paulo: Cantareira, MZUSP 591, 4521; São Paulo: Caxinguí, MZUSP 36116–7; São Paulo: Indianopolis, MZUSP 4550; São Paulo: Ipiranga, MZUSP 574, 2796; São Paulo: Santo Amaro, MZUSP 54399; São Paulo: Vila Galvão, MZUSP 4493; Santana do Parnaíba (23 26–46 55) MZUSP 42697; Santo André (23 41–46 26) MZUSP 4538, 4552, 8261–2.

URUGUAY: **Montevideo:** Montevideo (34 50–56 10) ZMB 7989(2)—possibly in error.

No data: ("Chile," in error) ZMH 02761–2 + x ray.

Anisolepis undulatus

ARGENTINA: **Buenos Aires:** *Dpto. La Plata:* Punta Lara, near La Plata (34 49–57 59) Koslowsky, 1895 (as *Anisolepis bruchi*).

BRAZIL: No additional data: ZMB 497 (type of *Laemanctus undulatus*), ZSM 504/0(2), ZMH 02765 + x ray. **Rio Grande do Sul:** No additional data: MCZ 84031–2, 84033: skeleton, 59273, MZUSP 541, 682, 2692–5, 2784–7, 2789, 2790, BMNH 86.10.4.4–5, 87.5.18.9 (syntypes of *Anisolepis iheringi*), ZMH 02755–6 + x rays; São Lourenço (now São Lourenço do Sul), southern border of Laguna dos Patos (31 22–51 58) BMNH 1946.8.5.90–1, MZUSP 548, 683, 2783, 2791–4, ZMB 3507(2).

URUGUAY: **Canelones:** Bañados near Carrasco (34 47–56 01) DZVU 280. **Paysandú:** Paysandú [?Department or city] (city: 32 19–58 04) USNM 65545–7. **San José:** Arazati (34 35–56 55) MHNM 2201; Pascual Beach, 4 km west of bus stop, Estero del Tigre (34 45–56 30) MHNM 3021.

Anisolepis longicauda

ARGENTINA: **Chaco:** *Dpto. Bermejo:* Mouth of the Río del Oro into the Río Paraguay (27 02–58 33) BMNH 91.6.17.1 [RR 1946.8.9.2] (syntypes of *Aptycholaemus longicauda*), MCZ 147353 + x ray

TABLE 1. MEASUREMENTS AND PROPORTIONS OF THE BODY, HEAD, AND TAIL OF *UROSTROPHUS* AND *ANISOLEPIS*. PROPORTIONS ARE BASED ON SPECIMENS THAT HAD ATTAINED AT LEAST 83% OF THE MAXIMUM KNOWN SNOUT–VENT LENGTH, BEYOND WHICH THERE APPEARS TO BE LITTLE ALLOMETRIC GROWTH. MEAN FIGURES ARE IN PARENTHESES. N = NUMBER OF SPECIMENS MEASURED. METHODS FOR TAKING MEASUREMENTS ARE GIVEN IN THE APPENDIX.

				Specimens ≥ 85% maximum S–V		
Species	Sex	N	Maximum S–V in mm	N	Tail as % of total length	Head as % of S–V length
U. vautieri	M	30	83	11	58(60)62	23(24.0)25
	F	47	108	8	56(58)59	21(22.5)24
U. gallardoi	M	8	75	6	64(66)76	23(24.7)26
	F	11	78	5	62(64)66	23(23.4)25
A. grilli	M	31	79	3	73(73)74	22(22.0)22
	F	36	97	13	69(71)72	20(21.3)23
A. undulatus	M	11	70	3	72(73)75	21(21.2)22
	F	28	88	6	69(71)73	19(19.8)21
A. longicauda	M	5	79	4	76(77)78	20(20.3)21
	F	8	98	7	73(74)75	19(20.1)22

TABLE 2. BODY SCALE COUNTS, BY SEXES, OF *UROSTROPHUS* AND *ANISOLEPIS*. MEAN FIGURES ARE IN PARENTHESES. N = NUMBER OF SPECIMENS EXAMINED. METHODS FOR COUNTING ARE GIVEN IN THE APPENDIX.

Species	Sex	N	Paravertebral scales	Midbody scales	Ventral scale rows
U. vautieri	M	24	99(117)14	78(87)106	—
	F	43	106(122)138	73(85)110	—
U. gallardoi	M	8	153(161)199	104(117)134	—
	F	11	136(157)178	104(115)123	—
A. grilli	M	21	103(122)139	70(85)106	17(19.4)23
	F	30	111(129)149	71(86)99	17(20.1)25
A. undulatus	M	11	99(104)110	78(79)80	13(15.5)17
	F	21	110(114)122	60(72)85	14(16.0)19
A. longicauda	M	5	107(131)153	78(87)100	15(15.5)16
	F	8	114(126)134	78(88)96	15(17.0)19

TABLES 3A AND 3B. HEAD SCALE AND FOURTH TOE LAMELLAE COUNTS OF *UROSTROPHUS* AND *ANISOLEPIS*. COUNTING METHODS ARE GIVEN IN THE APPENDIX. MEAN FIGURES ARE IN PARENTHESES. N = NUMBER OF SPECIMENS EXAMINED.

Species	N	Postrostrals	Between nasals	Between canthals	Supraorbital semicircles	Between semicircles
U. vautieri	76	3(5.1)6	5(6.0)6	4(6.3)8	7(9.1)11	0(1.0)2
U. gallardoi	21	5(5.7)6	5(6.4)8	7(8.0)11	8(9.9)13	1(2.0)3
A. grilli	55	4(5.5)7	5(6.4)8	6(8.8)11	9(11.0)14	1(1.3)3
A. undulatus	38	3(4.9)6	5(5.9)7	6(7.8)11	7(9.9)13	0(1.0)2
A. longicauda	13	4(5.0)5	6(6.0)7	7(8.1)10	9(10.2)13	1(1.9)3

Species	N	Between suboculars & supralabials	Supralabials	Infralabials	Temporals	Fourth toe lamellae
U. vautieri	76	0(0.7)1	6(7.3)9	6(7.8)10	7(8.9)11	21(24.2)30
U. gallardoi	21	0(0.9)1	7(8.7)10	8(10.6)13	11(12.4)14	22(26.2)29
A. grilli	55	0(1.0)2	6(8.1)10	6(8.4)11	8(10.4)14	22(22.5)30
A. undulatus	38	0(0.8)1	6(7.7)10	7(8.2)10	8(9.3)12	21(24.1)27
A. longicauda	14	1	7(8.0)9	8(8.8)10	10(12.0)14	20(23.3)26

TABLES 1A AND 1B. SKELETAL VARIATION IN *UROSTROPHUS* AND *ANISOLEPIS*. TOTAL CAUDAL VERTEBRAE ARE ACTUAL COUNTS, WITH MEAN VALUES IN PARENTHESES; ALL OTHERS ARE EXPRESSED AS THE PERCENTAGE OF THE TOTAL SAMPLE THAT POSSESSES EACH COUNT OR CONFIGURATION. COUNTING METHODS ARE GIVEN IN THE APPENDIX. N = NUMBER OF SPECIMENS EXAMINED.

Species	N	Sternal ribs		N	% Xiphisternal ribs					N	% Attached chevrons					N	% Unattached chevrons			N	% Isolated splints		N	% Total inscriptional ribs			
		2/2	3/3		1/1	0/0	2/2	2/3	3/3		2	3	4	5	6		2	3	4		0/0	1/1		10	11	12	13
U. vautieri	9	00	100	6	00	00	16	17	67	6	83	17	00	00	00	5	40	60	00	7	100	00	4	25	75	00	00
U. gallardoi	6	11	89	9	00	11	78	00	11	8	00	87	13	00	00	8	38	62	00	9	67	33	8	00	100	00	00
A. grilli	14	14	86	13	08	00	84	00	08	11	00	00	90	10	00	11	00	90	10	11	90	10	11	00	00	90	10
A. undulatus	3	33	67	3	00	00	100	00	00	5	00	00	80	00	20	5	00	100	00	3	100	00	3	00	00	67	33
A. longicauda	3	00	100	3	00	00	100	00	00	3	00	67	33	00	00	3	00	33	67	3	100	00	3	00	00	100	00

Species	N	% Total presacral vertebrae					N	% 1st cervical rib		N	% Lumbar vertebrae				N	Total caudal vertebrae	N	% Caudal transverse processes
		23	23/24	24	24/25	25		3	4		0/0	0/1	1/1	1/2				
U. vautieri	12	00	00	100	00	00	12	00	100	10	50	00	50	00	5	48(50)52	3	29(37)45
U. gallardoi	8	00	25	75	00	00	7	00	100	6	00	00	83	17	6	46(51)56	5	30(33)36
A. grilli	17	12	06	58	06	18	15	00	100	11	36	10	54	00	9	66(72)78	7	37(47)54
A. undulatus	3	33	00	33	00	33	3	100	00	3	100	00	00	00	3	70(71)72	2	70(71)72
A. longicauda	3	00	00	67	00	33	3	33	67	3	33	00	67	00	1	78	1	22

(syntype of *Aptycholaemus longicauda*); Colonia Benitez (27 20–58 57) BMNH 1902.2.10.1; *Dpto. San Fernando:* Resistencia (27 27–59 00) MACN 4025(2); Fontana (27 25–59 02) MACN 1187. **Misiones:** No additional data: MLP S.329–30, S.332, Koslowsky, 1895 (as *Anisolepis argentinus*). **Santa Fé:** No additional data: BMNH 98.11.3.1: skeleton.

PARAGUAY: No additional data: ZMB 10732(2), NMW 12971 + x ray; Primavera, "Alto Paraguay" (San Pedro) (24 34–56 35) BMNH 1955.1.5.84.

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APPENDIX: SCALE DEFINITIONS, MEASUREMENTS, AND COUNTS

We follow the useful scale definitions of Smith (1946) except in the instances below:

Pileus. All the dorsal head scales from the rostral to the occipital region when these are differentiated and large. Used in the sense of Friederich (1978).

Lorilabials. Scales below the loreals and suboculars and between these and the supralabials. Usually smaller than the loreals, but the loreals may vary much in size. The definition employed here is more restrictive than that of Smith (1946). As understood in this paper these scales are *not* adherent to the underlying periosteum, as are the loreals, but are, instead, lifted with the supralabials by forceps or dissecting needle, as the loreals cannot be.

Upper and lower temporals. Two levels of temporal scales distinguished by the planes—vertical or horizontal—in which they occur. The *lower temporals* lie in a vertical plane between orbit and ear. The *upper temporals* lie in a horizontal plane above the lower temporals, and may or may not be larger than the lower temporals, i.e., if supratemporals are, as defined by Smith (1946), necessarily larger than the lower temporals, these are *not* supratemporals. Usually the two sets of temporal scales are separated by a more or less enlarged double row of intertemporal scales that lie superficial to the postorbital-squamosal arch that is the inferior border of the upper temporal fossa of the skull.

Posterior auriculars. The scales posterior to the ear opening. In most taxa these are granular, but in some iguanians they are large and imbricate.

Sublabials. As used here these are equivalent to the "chin shields" of Smith (1946) and *not* synonymous with "sublabials" as defined by him. They are enlarged scales (="plates below the infralabials" in Van Denburgh, 1922, p. 46) medial to the infralabials on each side, the anteriormost usually in contact with the first infralabial. More posterior sublabials may or may not be in contact with the infralabials. Sublabials in the sense used here may be separated from the infralabials by one to several rows of smaller scales (=the "sublabials" of Smith = the "lateral gulars" of this paper).

Lateral gulars. Small scales—when present—between the plate-like sublabials and the comparably plate-like infralabials. These are distinguished from "central gulars"—the smaller scales medial to the sublabial series. When sublabials are not differentiated or at the point at which the sublabials become unrecognizable posteriorly, the distinction between lateral and central gulars ceases to be valid and these scales become simply "gulars."

Antehumeral-transverse gular fold. A transverse skin fold enclosing markedly reduced scales, crossing the posterior gular region and on each side continuing up and over the forelimb insertion as an antehumeral fold.

Pregular fold. A transverse skin fold across the middle or anterior gular region, not enclosing markedly reduced scales.

Counts of the scales of the head, body, and digital lamellae were taken as follows:

Postrostrals. All scales in direct contact with rostral between anterior supralabials.

Between nasals. All scales crossed by a line drawn horizontally between the midpoints of the nasal scales.

Between canthals. All scales crossed by a line drawn horizontally between the anterior extremities of the posterior canthals.

Supraorbital semicircles. Enlarged scales in the supraorbital arc beginning with the first in contact with the posterior canthal.

Between supraorbital semicircles. Minimum number of scales between semicircles at their closest approach.

Between subocular(s) and supralabials. Minimum number of scales between subocular(s) and supralabials at their closest approach.

Supralabials. Counted back from the rostral to, and including, the most posterior scales that take part, however slightly, in the margin of the mouth.

Infralabials. Counted back from the mental to, and including, the most poste-

rior scale that takes part, however slightly, in the margin of the mouth.

Temporals. Number of scales crossed by a line drawn horizontally across the temporal region, between the postorbital(s) and the anterior border of the external ear.

Paravertebrals. Number of scales crossed by a line drawn just to the left of the midline between the posterior parietal scales and a line drawn horizontally across the back even with the anterior margins of the hindlimb insertions.

Midbody scales. Number of scales around the body midway between the forelimb and hindlimb insertions.

Ventral scale row. Number of large, keeled ventral scales crossed by a line drawn horizontally across the belly halfway between the forelimb and hindlimb insertions (*Anisolepis* only).

Fourth toe lamellae. Number of scales on the ventral surface of the fourth toe, beginning with the first scale below the free proximal part of the digit and counting to, but not including, the scale just posterior to the claw.

Snout–vent length. Measured from the anterior margin of the rostral scale to the anterior border of the vent.

Measurements were taken as follows:

Tail length. Measured from the anterior margin of the vent to the distal extremity of the tail.

Head length. Measured from the anterior margin of the rostral scale to the middle of the inferior border of the tympanum (the latter marking the center of the articular fossa of the articular bone).

Serial homologues of the axial skeleton were counted as follows:

Presacral vertebrae. Counted as all vertebrae anterior to the first sacral, including the atlas. Asymmetrical counts such as 23/24 or 24/25 are due to an asymmetrical sacrum.

First cervical rib. Counting the atlas as the first vertebra, the number of the most anterior vertebra to bear a pair of ribs, the third or fourth in this group.

Lumbar vertebrae. The number of vertebrae immediately anterior to the first sacral vertebra from which ribs are entirely lacking; asymmetrical counts such as 0/1 indicate the absence of a rib on one side.

Total caudal vertebrae. The total number of vertebrae between the posterior sacral vertebra and the distal extremity of the tail.

Caudal transverse processes. The number of anterior caudal vertebrae that bear at least some trace of transverse processes; since the processes may become smaller gradually, determination of the exact vertebra of disappearance may be subjective.

Sternal ribs. The number of inscriptional ribs that join bony dorsal ribs to the lateral margin of the sternum.

Xiphisternal ribs. The number of inscriptional ribs that join bony dorsal ribs to the xiphisternal rods; "lf" indicates the presence of free posterior extensions of the xiphisternal rods beyond the xiphisternal rib.

Attached chevrons. The number of continuous inscriptional chevrons that join the bony dorsal ribs, posterior to the xiphisternum.

Unattached chevrons. The number of inscriptional chevrons that are continuous midventrally but do not reach the distal extremities of their corresponding bony dorsal ribs.

Isolated splints. Calcified cartilages within the inscriptions of the myomeres, not connected midventrally, nor to the bony dorsal ribs above.

Total inscriptional ribs. The total number of inscriptional ribs beginning with the most anterior sternal rib and counting back to include the xiphisternal ribs, chevrons, and splints. The number actually represents the number of postcervical inscriptional ribs, as short inscriptional ribs are also present on the bony ribs anterior to the first attached to the sternum.

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The Neotropical Orb-Weaver Genera Edricus and Wagneriana (Araneae: Araneidae)

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THE NEOTROPICAL ORB-WEAVER GENERA *EDRICUS* AND *WAGNERIANA* (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. *Edricus* and *Wagneriana* species are Neotropical, nocturnal orb weavers. *Edricus* species are found from Mexico and Panama to Ecuador. Most *Wagneriana* species are found in the Amazon area and southeastern South America. Because of the similarity of the structure of male and female genitalia and the presence of a paramedian apophysis in the male palpus, they are related to *Alpaida*, *Eriophora*, *Parawixia*, and *Verrucosa*.

There are two species of *Edricus*, both previously known from only one sex, and 39 species of *Wagneriana*, 26 of them new. That is, only one-third of the species were previously known. *Anawixia* Chamberlin and *Paraverrucosa* Mello-Leitão are subjective synonyms of the name *Wagneriana*. Eight species names are synonymized.

INTRODUCTION

This is one of a series of papers authored by Levi through the period 1968–1990 intended to make it possible to identify Neotropical orb weavers. The araneid orb weavers are the third largest spider family with 2,600 named species world-wide (Platnick, personal communication, 1989). About one-third of the Neotropical orb-weaver species have now been revised. Despite the popularity of orb weavers as research subjects in studies of behavior, ecology, and silk production, identification has been severely hampered because the descriptions of species are scattered through old literature and were made (as is unfortunately still sometimes done) without reference to or comparison with previously described species. Some had been placed in wrong genera and frequently males and females were described under different names. A future goal of these studies is the analysis of interrelationships among genera. This can be done only by examining and comparing all species of each genus and only after most of the genera are revised.

Revised here are the genera *Edricus* and *Wagneriana* which share a similar abdomen shape and similar genitalia, both synapomorphies. The species of the two genera have been confused despite their distinctive carapace and sternum shapes.

Only one common species of *Wagneriana* was previously readily recognized, *W. tauricornis*, common in Florida. Roewer (1942) and Bonnet (1959) list four other species. The collections available included 39 different species, some of which had been placed in other genera of the family.

METHODS AND MATERIALS

The methods were the same used in my previous papers: careful comparison of the structures of the genitalia of males and females made by illustrating them to separate species. The features that make the genus distinct are also illustrated, although a careful comparison of genera has to wait until the species of more of them are known. Species descriptions cite the distinguishing features and the localities where specimens have been found. Despite this, problems invariably remain. Some of them can be resolved by studying specimens, others by using more sophisticated methods. (But molecular studies

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would be inappropriate for this study, as they would not facilitate recognition or placement of specimens into the species or matching of names with specimens.) Remaining problems are that some species can be clearly recognized in one sex only (e.g., there are difficulties in separating females of *W. jelskii*, *W. maseta*, and *W. transitoria*, also females of *hassleri* and *silvae*). Another persistent problem is whether differences between specimens from different places represent species differences or geographical variation (e.g., *W. huanca*, Figs. 149, 150). In some cases the association of males with females may remain uncertain (e.g., *W. taim*).

Eye ratios. The diameters of the posterior median eyes and lateral eyes as seen in profile are measured by comparison with the diameter of the anterior median eye as seen in profile. The distances between the borders of the anterior median eyes and between the anterior median eyes and anterior lateral eyes are measured by comparison with the diameter of the anterior median eyes in profile. The distances between the posterior median eyes and between the posterior median eyes and posterior lateral eyes are measured by the comparison with the diameter of the posterior median eyes as seen in profile. The method was first suggested by H. Homann (personal communication) as an alternative to giving absolute measurements or reporting the fractions as read in a micrometer. However, the measurements here and those in my other araneid papers are only rough calculations as araneid specimens of the same species are quite variable in their eye diameter and placement, and commonly one or two eyes are deformed or missing (e.g., the anterior median eyes of the holotype of *W. janeiro* are absent).

Internal female genitalia. Illustrations were made by mounting the epigynum temporarily in Hoyer's medium on a microscope slide, the dorsal side facing up. Since *Wagneriana* epigyna are lightly sclerotized and relatively flat they are easier to examine than the epigyna of species of other genera.

Paratypes and holotypes. Other than the holotype and doubtful specimens, all specimens examined of a new species are marked and reported as paratypes. This permits wide distribution of paratypes to museums in Central and South America and will facilitate future identification of specimens. Holotypes are deposited in a museum with a professional arachnologist as curator or may have to be returned to the country where collected. Rarely is the specimen illustrated or described not the holotype, but if the holotype is in poor condition, a better specimen was used for description and illustration. If an adequate illustration was made earlier I did not make another even if better specimens of the same species were found later. The holotypes of previously named species have been examined and illustrated over a period of twenty years because many had been misplaced. (Misplaced specimens are a unique problem of revising a very large family.) Some specimens for which my information was incomplete could not be borrowed a second time (those of the Caracas and Rio de Janeiro museums).

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- CAS California Academy of Sciences, San Francisco, United States; W. J. Pulawski, D. Ubick
- CNC Canadian National Collections, Ottawa, Canada; C. Dondale

CUC	Cornell University Collection, kept in the AMNH; N. Platnick
DU	D. Ubick
EMUCB	Essig Museum, University of California Berkeley, California, United States; E. I. Schlinger, C. E. Griswold
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards
IBNP	Inventario Biológico Nacional, San Lorenzo, Paraguay; J. A. Kochalka
IMPR	I. M. P. Rinaldi, Rio Claro, Est. São Paulo, Brazil
INPA	Instituto Nacional de Pesquisas da Amazonia, Manaus, Est. Amazonas, Brazil; J. A. Raphael, H. Höfer
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert
JAK	John A. Kochalka
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury
MCN	Museu de Ciências Naturais, Porto Alegre, Rio Grande do Sul, Brazil; A. Lise, E. Buckup
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, United States
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; L. Avilés
MEG	M. E. Galiano
MHNC	Museu de História Natural, Capão da Imbuia, Curitiba, Paraná, Brazil; L. Bittencourt, S. de Fátima Caron
MHNM	Museo de Historia Natural de Montevideo, Uruguay; R. M. Capocasale
MHNMC	Museo de Historia Natural, Medellín, Colombia; Marco A. Serna D.
MHNSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marco's, Lima, Peru; D. Silva D.
MIUP	Museo de Invertebrados, Universidad de Panamá, Panama City, Panama; D. Quintero A.
MLP	Museo, Universidad Nacional de La Plata, La Plata, Argentina; R. F. Arrozpide
MNRJ	Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa
MNHN	Muséum National d'Histoire Naturelle, Paris, France; J. Heurtault
MNSD	Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic; B. C. Reynoso S.
MPM	Milwaukee Public Museum, Milwaukee, Wisconsin, United States; J. P. Jass
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; P. Vanzolini, L. Neme, J. L. M. Leme
MZUF	Museo Zoologico, Università, Florence, Italy; S. Mascherini
NHMW	Naturhistorisches Museum, Wien, Austria; J. Grüber
NMB	Naturhistorisches Museum, Basel, Switzerland; E. Sutter
NRMS	Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt
PAN	Polska Akademia Nauk, Warszawa, Poland; A. Riedel, W. Starega, J. Proszynski, A. Slojewska, E. Kierych
REL	R. E. Leech
SJ	Steve Johnson
SMF	Natur-Museum und Forschungs-Institut, Senckenberg, Frankfurt am Main, Germany; M. Grasshoff
UCR	University of California, Riverside, California, United States; S. I. Frommer
USNM	National Museum of Natural History, Smithsonian Institu-

tion, Washington, D.C., United States; J. Coddington
YDL Y. D. Lubin
ZMK Zoologisk Museum, Copenhagen, Denmark; H. Enghoff
ZSM Zoologische Staatssammlung, Munich, Germany

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Edricus O. P.-Cambridge

Edricus O. P.-Cambridge, 1890: 57. Type species *Edricus spinigerus* by monotypy. The generic name is masculine (Bonnet, 1956: 1647).

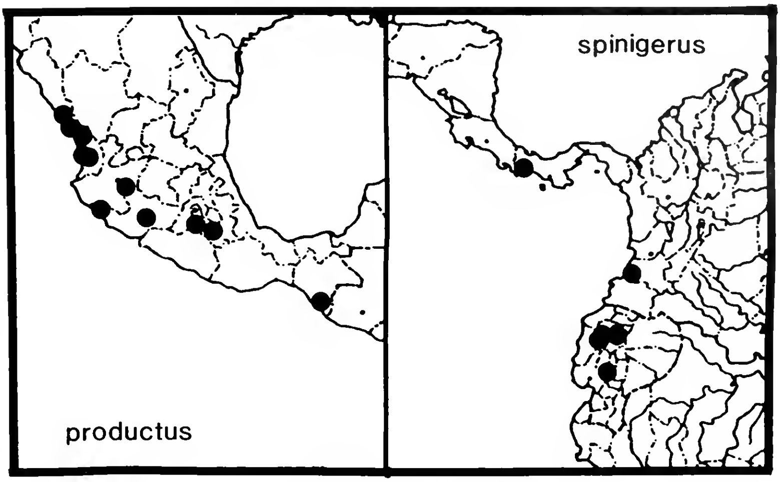
Note. The literature is confused because females of the common *Witica crassicauda* (Keyserling) were erroneously matched with *Edricus* males and placed in the genus *Edricus*. Also several *Alpaida* (see list below) species had been described in *Edricus*.

Diagnosis. Unlike those of related genera and most other araneids, the carapace and sternum of *Edricus* are modified. The carapace in both sexes is elongated and narrowed in the thoracic region (Figs. 3, 7, 11, 14) and the sternum is posteriorly narrowed and elongated (Figs. 4, 8, 12, 15). Unlike those of most other araneids, except *Pronous*, the posterior median eyes of *Edricus* are almost 1.5 to 2 times the diameter of the anterior medians (Fig. 5). The height of the clypeus equals three to four diameters of the anterior median eyes (Fig. 5). The prosomal modifications, the high clypeus and the large posterior median eyes are synapomorphies for the two species of *Edricus*. Unlike that of *Wagneriana* the palpus has a paramedian apophysis in the shape of a toad-stool on its side (PM in Figs. 6, 13). The fourth leg is as long as or longer than the first, another synapomorphy for the two species. (The fourth leg is also longer than the first in the unrelated *Micrathena* species, Levi, 1985.)

Description. Carapace, chelicerae, endites, sternum orange-brown. Coxae orange to orange-brown. Legs orange-brown. Abdomen with some black and white pigment. Carapace without macrosetae. Abdomen with four pairs of lateral tubercles and three posterior median ones. In males the anterior lateral tubercles are prominent spines (Figs. 7, 14). The shape of the abdomen with pairs of tubercles and posterior median tubercles (Fig. 3, 11) resembles that of *Wagneriana*. The epigynum has a median lobe (Figs. 1, 9) also resembling that of *Wagneriana*. Both these similarities are regarded as synapomorphies.

Epigynum small with a posterior median plate that differs in shape in the two species (Figs. 2, 10). Male palpal patella with one macroseta. The male of *E. productus* has a tooth on the endite and a hook on the first coxa (Fig. 8), *E. spinigerus* has lost both. *Edricus productus* has a macroseta on the fourth trochanter, *E. spinigerus* does not. The second tibia has a small spur with one or two macrosetae in males of *E. productus* (Fig. 7), with one macroseta in *E. spinigerus* (Fig. 14). The palpus is similar in structure to that of *Wagneriana* species. The conductor is on the ventral face of the palpus as in *Wagneriana*, *Parawixia*, and *Alpaida* (not near the rim as in *Araneus*).

Distribution. There are only two species, one in Mexico, the other in Central America to Ecuador (Map 1).



Map 1. Distribution of *Edricus* species.

Misplaced Species

Edricus atomarius (Simon, 1895); Roewer, 1942: 761 is *Alpaida atomaria* (Simon). See Levi, 1988: 458.
E. cayana (Taczanowski, 1873); Roewer, 1942: 762 is *Witica cayana* (Taczanowski). See Levi, 1986: 44.
E. crassicauda (Keyserling, 1865); Roewer, 1942: 762 is *Witica crassicauda* (Keyserling). See Levi, 1986: 41.
E. ensifer di Caporiacco, 1947: 25 is *Alpaida truncata* (Keyserling). See Levi, 1988: 472.
E. eupalaestris Mello-Leitão, 1943: 177 is *Wagneriana eupalaestris* (Mello-Leitão).
E. tricuspis (Getaz, 1893); Roewer, 1942: 762 is *Witica crassicauda* (Keyserling). See Levi, 1986: 41.
E. truncatus (Keyserling, 1865); Roewer, 1942: 762 is *Alpaida truncata* (Keyserling). See Levi, 1988: 472.

Unrecognizable species

Edricus rubricornis Mello-Leitão, 1940: 204. Female holotype from Colatina, Espírito Santo, Brazil (MNRJ), lost.

KEY TO *EDRICUS* SPECIES

1. Females 2
– Males 3
2(1). Posterior median plate of epigynum in posterior view almost as long as wide (Fig. 2); Mexico (Map 1) .... *productus*
– Posterior median plate of epigynum in posterior view about twice as wide as long (Fig. 10); Panama to Ecuador (Map 1) .... *spinigerus*
3(1). Third coxa separated from fourth by about their diameter (Fig. 8); palpus with median apophysis rounded laterally (Fig. 6); Mexico (Map 1) .... *productus*
– Third coxa adjacent to fourth (Fig. 15); palpus with median apophysis angular laterally (Fig. 13); Panama to Ecuador (Map 1) .... *spinigerus*

Edricus productus O.P.-Cambridge
Figures 1–8; Map 1

Edricus productus O. P.-Cambridge, 1896: 186, pl. 23, fig. 5, ♂. Male holotype from Cuernavaca, Morelos State, Mexico, in BMNH, examined. F. P.-Cambridge, 1904: 500, pl. 49, fig. 26, ♂. Roewer, 1942: 762. Bonnet, 1956: 1648.

Description. Female from Escuintla, Chiapas. Sternum orange with median white streak. Venter of abdomen with a pair of white blotches framed by black. Posterior median eyes 1.5 diameters of anterior medians, anterior laterals 0.9 diameter, posterior laterals 1 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 2.5 diameters apart. Abdomen as in Figure 3. Total length 15 mm. Carapace 6.3 mm long, 2.8 mm wide. First femur 3.5 mm; patella and tibia 4.1 mm; metatarsus 2.6 mm; tarsus 1.1 mm. Second patella and tibia 3.5 mm; third, 2.5mm. Fourth femur 4.5 mm; patella and tibia 4.4mm; metatarsus 3.1 mm, tarsus 1.0 mm.

Male from Tepic, Nayarit. Posterior me-

dian eyes 1.5 diameters of anterior medians, anterior laterals 0.8 diameter, posterior laterals 1 diameter. Anterior median eyes 1.8 diameters apart. Posterior median eyes 2 diameters apart. Endite with tooth, palpal femur with indistinct tooth. First coxa with hook (Fig. 8). Fourth trochanter with one macroseta. Second tibia thicker than first and with distal spur bearing one macroseta on right leg, two on left leg (Fig. 7). Abdomen like that of female but with anterior pair of spines slightly sclerotized (Fig. 7). Total length 9.6 mm. Carapace 5.4 mm long, 2.3 mm wide. First femur 3.5 mm; patella and tibia 4.0 mm; metatarsus 2.8 mm; tarsus 1.1 mm. Second patella and tibia 3.4 mm; third, 2.3 mm. Fourth femur 3.7 mm; patella and tibia 3.9 mm; metatarsus 2.9 mm; tarsus 1.8 mm.

Illustrations. The illustrations were made from a female from Escuintla, Chiapas, and from a male from Tepic, Nayarit.

Variation. The abdomen shape is quite variable in females, especially its width and the size of the spines. Total length of females 11.7 to 18.5 mm, of males 9.5 to 9.6. The male from Puebla had only one macroseta on the spur of the tibia.

Diagnosis. Females differ from *E. spinigerus* by the posterior median plate of the epigynum being as wide as long (Fig. 2) and the outline of the carapace (Fig. 3). The male differs by the folding of the distal end of the median apophysis (Fig. 6) and the shape of the sternum (Fig. 8). The fourth trochanter has a macroseta, lacking in *E. spinigerus.*

Records. MEXICO *Sinaloa:* Mazatlan, 6 Sept. 1956, ♀ (A. F. Archer, AMNH), 2 Sept. 1977, ♀ (C. E. Griswold, EMUCB); La Concordia, N Copala, 610 m, 10 Sept. 1979, ♀ (D. E., J. A. Breedlove, CAS); 32 km E Villa Union, 19 Sept. 1964, imm. (E. I. Schlinger, UCR). *Nayarit:* San Blas, 17–21 Sept. 1953, ♀ (B. Malkin, AMNH); Acaponeta, 29 Nov. 1939, imm. (H. Bogert, N. E. Vokes, AMNH); Tepic, ♂ (MCZ), 15 Sept. 1953, 2♂ (B. Malkin, AMNH), 2–7 Aug. 1963, imm. (C., M. Goodnight, B. Malkin, AMNH); 8 km NW Tepic, 13 May 1963, imm. (W. J. Gertsch, W. Ivie, AMNH). *Jalisco:* Lago de Chapala, 16 July 1976, ♀ (J. Harp, R. Mitchell, SJ). *Colima:* 19 km E Manzanillo, 11 May 1963, imm. (W. J. Gertsch, W. Ivie, AMNH). *Michoácan:* 16 km S Uruapan, 6 July 1985, ♂ (Woolley, Zolnerovich, MCZ). *Puebla:* 0.8 km E Tepexco, 1,250 m, 24 Aug. 1977, ♂ (E. I. Schlinger, EMUCB). *Chiapas:* Escuintla, ♀ (Crawford, MCZ).

Edricus spinigerus O. P.-Cambridge
Figures 9–15; Map 1

Edricus spinigerus O. P.-Cambridge, 1890: 58, pl. 4, fig. 1, ♂. Male holotype from Bugaba, Panama, in BMNH, examined. Keyserling, 1892: 33, pl. 2, fig. 30, ♂. F. P.-Cambridge, 1904: 500, pl. 49, fig. 25, ♂. Roewer, 1942: 762. Bonnet, 1956: 1648 [*spiniger*].

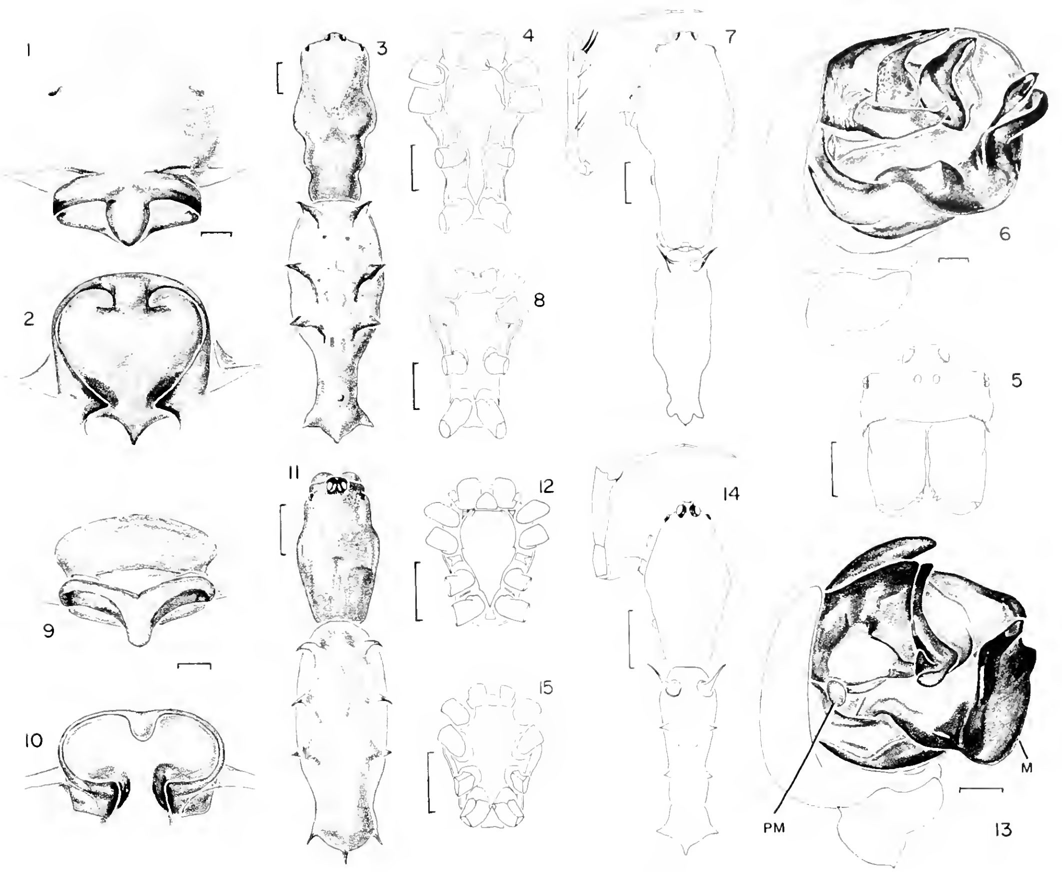
Description. Female from Ecuador. Legs orange-brown with indistinct, dusky longitudinal streaks. Venter of abdomen black between epigynum and spinnerets with a white line on each side, white bordered with black on each side behind spinnerets. Posterior median eyes 2.2 diameters of anterior medians, anterior laterals 0.9 diameter, posterior laterals 0.9 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.1 diameters apart. Abdomen as in Figure 11. Total length 8.0 mm. Carapace 3.0 mm long, 1.6 mm wide. First femur 2.5 mm; patella and tibia 2.7 mm; metatarsus 1.9 mm; tarsus 1.0 mm. Second patella and tibia 2.3 mm; third, 1.7 mm. Fourth femur 3.0 mm; patella and tibia 3.1 mm; metatarsus 2.1 mm; tarsus 0.9 mm.

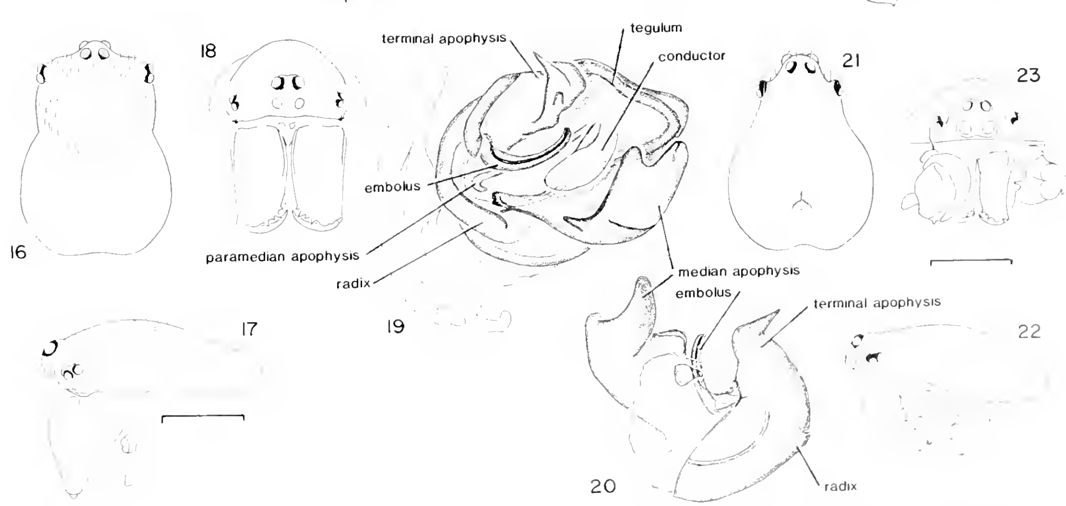
Male from Depto. Cauca, Colombia. Coxae brown; legs dusky orange. Posterior median eyes 1.6 diameters of anterior me-

→

Figures 1–8. *Edricus productus* (O. P.-Cambridge). 1–5. Female. 1. Epigynum, ventral. 2. Epigynum, posterior. 3. Dorsal. 4. Sternum and coxae. 5. Eye area and chelicerae. 6–8. Male. 6. Left palpus. 7. Dorsal with second leg. 8. Sternum and coxae.

Figures 9–15. *E. spinigerus* (O. P.-Cambridge). 9–12. Female. 9. Epigynum, ventral. 10. Epigynum, posterior. 11. Dorsal. 12. Sternum and coxae. 13–15. Male. 13. Palpus. 14. Dorsal with second leg. 15. Sternum and coxae.





Figures 16–23. *Wagneriana* anatomy. 16–18. *W. tayos* n. sp., female. 16. Carapace, dorsal. 17. Carapace, chelicera, lateral. 18. Eye area and chelicerae. 19–20. *W. transitoria*, left palpus. 21–23. *W. tayos* n. sp., male. 21. Carapace, dorsal. 22. Carapace and chelicerae, lateral. 23. Eye area, chelicera, and right palpus.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

dians, anterior laterals 0.8 diameter, posterior laterals 0.8 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.4 diameters apart, 1.3 diameters from laterals. Endite without tooth. First coxa without hook. Fourth trochanter without macroseta. Second tibia thicker than first, with a distal spur and one macroseta (Fig. 14). Total length 6.5 mm. Carapace 3.0 mm long, 1.5 mm wide. First femur 2.4 mm; patella and tibia 2.7 mm; metatarsus 2.0 mm; tarsus 1.0 mm. Second patella and tibia 2.1 mm; third, 1.6 mm. Fourth femur 2.7 mm; patella and tibia 2.7 mm; metatarsus 2.1 mm; tarsus 0.8 mm.

Illustrations. The illustrations were made from specimens from Pichincha Province, Ecuador.

Variation. Total length of females 8.0 to 10.2 mm, of males 6.5 to 7.1.

Diagnosis. The female can be separated from that of *E. productus* by the shape of the epigynum, wider than long in posterior view (Fig. 10), and by the different outline of the carapace (Fig. 11). The male is separated by the shape of the distal end of the median apophysis (Fig. 13), by the outline of the sternum (Fig. 15), and by the lack of a macroseta on the fourth trochanter.

Natural History. The specimens from Tinalandia were collected by beating vegetation. Lubin (personal communication, 1989) found an immature in a nearly vertical web, 10 cm in diameter, 5 cm above ground. The adult female was a meter away, an immature male in a similar-sized web 5 to 10 cm above ground and 10 cm in diameter. The web was symmetrical with an open hub, the female sat cephalic region down in the hub. Another male and female were collected sitting together under a leaf about 10 cm from the female's web.

Records. COLOMBIA *Cauca:* Pacific coastal plain NW Guapi, Jan. 1973, ♂ (W. Eberhard, MCZ). ECUADOR *Pichincha:* Río Palenque, km 47 on Santo Domingo-Quevedo Road, 150 m, 15 Mar. 1982, ♀, ♂, imm. (Y. Lubin YDL 383, MCZ); Río Pilatón, ♀ (G. W. Prescott, MCZ); Tinalandia, 12 km E Santo Domingo de los Colorados, 750 m, 11–17 May 1986, ♀, ♂ (G. B. Edwards, FSCA); 47 km S Santo Domingo, Río Palenque Sta., 18–30 May 1975, ♂ (S., J. Peck, CNC). *Bolívar:* Balzapampa, 700 m, 28 May 1938, ♀ (W. Clarke-Macintyre, AMNH).

Wagneriana F. P.-Cambridge

Wagneria McCook, 1894: 203. Type species by monotypy *Epeira tauricornis* O. P.-Cambridge. The name is preoccupied by *Wagneria* Robineau-Desvoidy, 1830, for a dipteran, and by Gistl, 1848, for a mollusk (Neave, 1940: 650).

Wagneriana F. P.- Cambridge, 1904: 497. New name for *Wagneriana* McCook, preoccupied. The name is of feminine gender.

Anawixia Chamberlin, 1916: 258. Type species by monotypy and original designation *A. atopa* Chamberlin, 1916: 258 [= *W. transitoria* (C. L. Koch)]. NEW SYNONYMY.

Paraverrucosa Mello-Leitão, 1939a: 64. Type species by monotypy and designation *P. neglecta* Mello-Leitão, 1939a: 65. NEW SYNONYMY.

Diagnosis. The carapace is high, the cephalic region slightly swollen behind the eyes (Figs. 18, 23), and in the female the sides of the thoracic region are usually glabrous, often dark (Figs. 16, 27, 38, 63). The carapace of the female may have a pair of macrosetae or more in the thoracic groove (Figs. 32, 38; Levi, 1976, figs. 62, 63, 64, 67). The glabrous often dark sides of the carapace as well as the macrosetae in the thoracic groove are synapomorphies of the species of *Wagneriana*. The macrosetae may be absent, perhaps secondarily lost. The paramedian apophysis of the male palpus is an L-shaped rod (Fig. 19), lying on its side, rarely rounded (U-shaped) or with an acute angle (V-shaped), a synapomorphy shared by all species of *Wagneriana* but not so in *Edricus* species. The terminal apophysis and embolus are fused (Figs. 19, 20). Another synapomorphy of *Wagneriana* species is the modification of the base of the median apophysis above the radix; it may have a small depression (Fig. 28) or teeth (Fig. 19), but lacks the large concavity of the median

apophysis of males of *Eriophora* and *Parawixia*. In most genera of araneids the attachment of the median apophysis is not modified; it may be a sclerotized bar or may not be sclerotized.

Description. The coloration of all species is about the same: carapace, sternum, legs yellowish to orange-brown. Carapace often with dusky marks and sides of thoracic region usually, but not always, dark and shiny, and cephalic region with some white setae (Fig. 63). Sternum always darker than coxae. Legs usually with indistinct dusky rings. Abdomen spotted with shades of brown, usually without folium often with dark median band (Figs. 57, 86); no two specimens of a species are identical. Venter gray to black with indistinct white marks. All *Wagneriana* species have a narrow, soft abdomen, longer than wide with nine to 15 tubercles (Figs. 27, 70, 153), three pairs anterior and middle on sides, one pair posterior on sides, and two or three in a posterior, median line (the most posterior tubercle above the spinnerets, which may face posteriorly or ventrally, may be lacking). The most anterior pair of tubercles may be double in *W. uzaga*, *W. spicata*, *W. gavensis*, and *W. iguape* and this is consistent in all specimens of several species (Figs. 126, 128, 132). The tubercles of some specimens of several species may be sclerotized spines. There is no median anterior tubercle (except in *W. turrigera* [Figs. 203, 204], which may not belong here). The position of the tubercles of the abdomen is a synapomorphy shared with *Edricus* and *Parawixia* species. The abdomen may be truncate behind the spinnerets (Fig. 64) or may have a postanal tail (Fig. 66); both shapes may be found in different specimens of the same species. Posterior median eyes usually slightly smaller than anterior medians, laterals the smallest (Figs. 17, 18).

Another apomorphy of *Wagneriana* species shared with *Edricus* is the shape of the epigynum, a wide median lobe often with a minute, light scape at its tip (Figs. 24, 45). It is not rebordered and lacks a median anterior notch (or pocket) as in *Alpaida* (a pocket is present in *W. yacuma*, Fig. 172, and the epigynum is rebordered in *W. gavensis*, Fig. 134). Posteriorly the epigynum has a median plate and two lateral plates, the lateral plates continue ventrally and form the wide median lobe in ventral view (Figs. 25, 30). The seminal receptacles of all females were illustrated, although it is not known whether this will be useful. They are easily examined unlike those of some other araneid genera. The receptacles of some species are consistently thin-walled (Fig. 125), others thick-walled (Fig. 118).

In males the carapace is much narrower in front than in females, high in the thoracic region, with few short setae and lateral eyes not on tubercles (Figs. 21–23). All males have one patellar macroseta on the palpus; endite has a large tooth (Figs. 22, 23) facing a tubercle on proximal end of palpal femur. First coxa with a distal, ventral hook (Figs. 22, 23) and in larger species with a dorsal tubercle that fits against the carapace rim. As in *Parawixia* and *Wixia* some species have one or more macrosetae on fourth trochanter. Second femur (sometimes also third and fourth, rarely first) with ventral row of macrosetae. In all species second tibia thicker than first, more or less swollen, with short, strong macrosetae. Abdomen similar to that of female but smaller (Fig. 128).

The terminal apophysis and embolus are fused (Figs. 19, 20). The terminal division, the terminal apophysis and embolus, is a triangular structure, fan-shaped, its outer edge modified in various species. The fan-shaped terminal division is a synapomorphy shared with *Edricus* and *Parawixia* species. Some female individuals have lost the macrosetae on the carapace and some males have lost the macrosetae on the fourth trochanter (in species that normally have them). In all species there is considerable individual variation in markings and in color, size, length, and prominence of tubercles, and the length of the postanal tail. Two species always have the tubercles

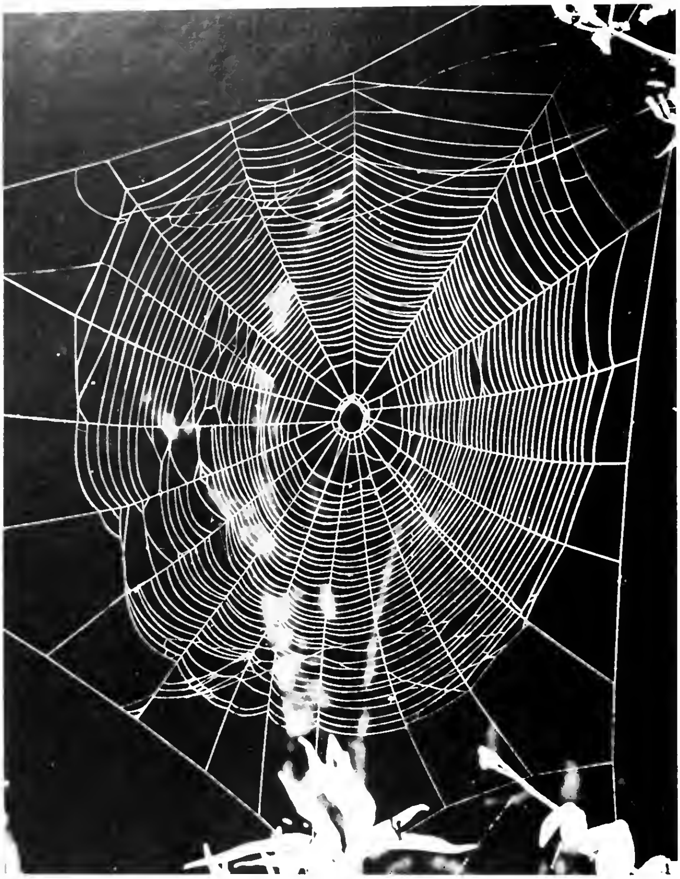


Plate 1. Web of *Wagneriana undecimtuberculata*, horizontal diameter of orb 26 cm (photo W. Eberhard).

drawn out: *W. grandicornis* (Figs. 65, 66) and *W. heteracantha* (Fig. 108). Only one species, *W. neglecta*, consistently has a long tail (Figs. 119, 122). Most species are surprisingly similar in appearance and can not be separated by color pattern or body shape; they have to be separated by the genitalia.

Natural History. All species make a complete orb web and hang cephalic region down in the middle. There is no retreat (Plate 1).

W. Eberhard (personal communication) found that *W. tauricornis* and *W. undecimtuberculata* take their web down when not in use (usually but not always in the daytime) and then sit at exposed sites like the tips of thin branches with their legs pressed to their bodies. Their irregular outlines make them hard to recognize as a spider. When they have an orb they generally hang in the hub or sit on one of the frame or anchor lines facing away with a line to the hub held by leg IV.

Distribution. All species are Neotropical. Only *W. tauricornis* extends its range into more temperate North America, and *W. spicata* is found in Mexico. Most species are found in the Amazon drainage and southeastern South America (Maps 2–4).

Doubtful placement

One species, *W. turrigera*, has been placed in *Wagneriana* for convenience; it may have to be placed

in a new genus when males are found. *Wagneriana turrigera* differs from other *Wagneriana* by having a low carapace and a long anterior median projection from the abdomen (Figs. 200–204).

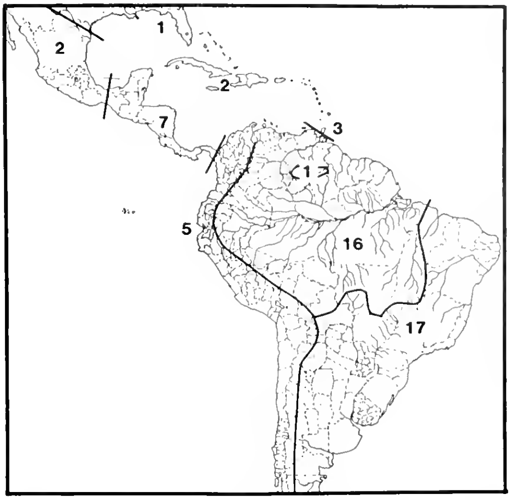
The separation and determination of specimens of *W. heteracantha*, *W. neglecta*, and *W. eupalaestris* remains uncertain, as is the separation of the females of *W. transitoria*, *W. jelskii*, *W. maseta*, and *hassleri* and *silvae*.

Misplaced species

Wagneriana minutissma Mello-Leitão, 1941: 250. Male holotype from Rio Negro, total length 1.5 mm, MNRJ no. 58298, is a *Kaira*.

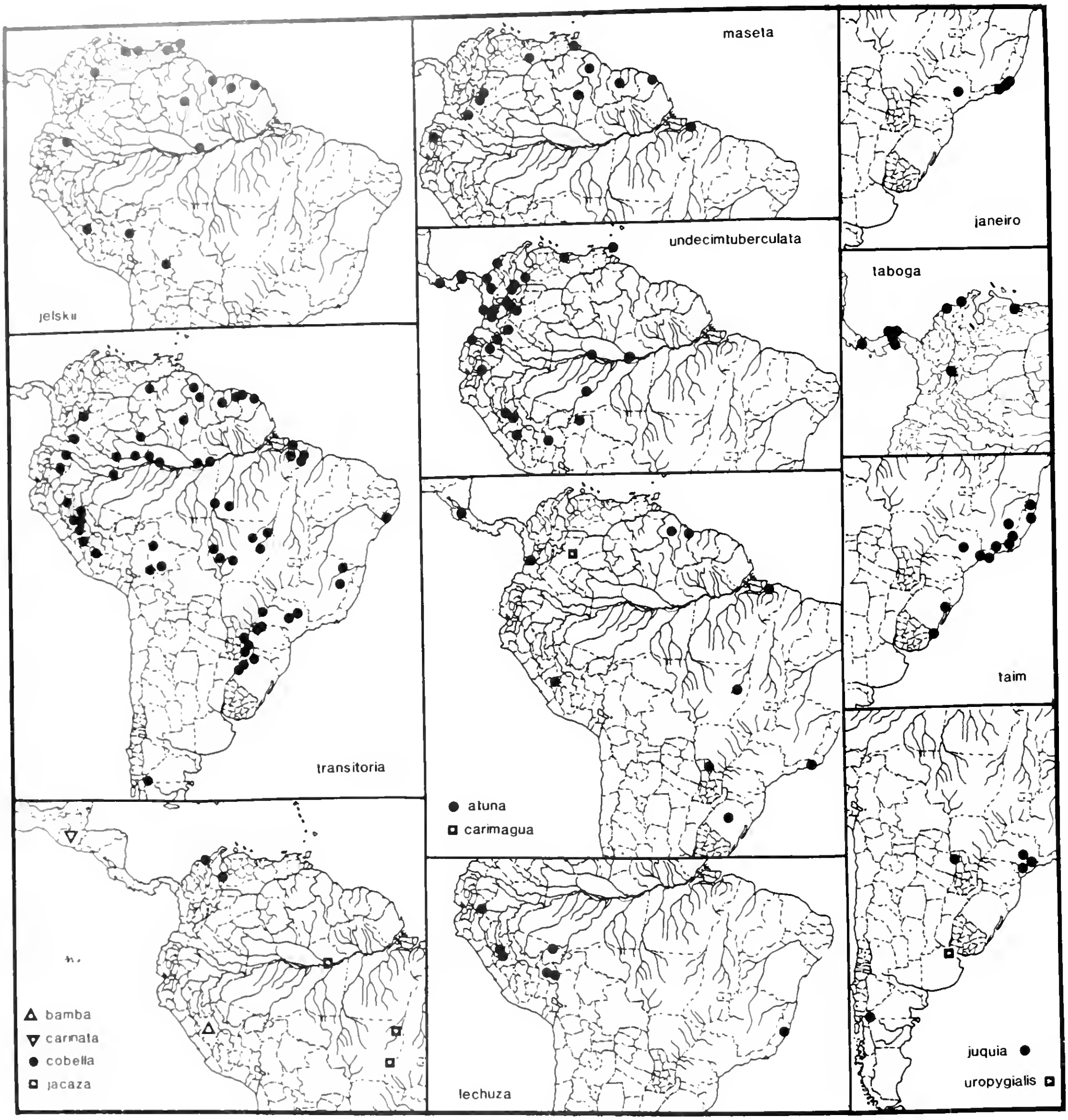
Key to female *Wagneriana*

1. Anterior pair of tubercles of abdomen double (Figs. 132, 138, 143) 2
– Anterior pair of tubercles single (Figs. 27, 32, 38) 5
2(1). Thoracic region with two macrosetae, (Fig. 132); Mexico to Costa Rica (Map 4) .... *spicata*
– Carapace without macrosetae (Figs. 138, 143); southeastern Brazil to Paraguay 3
3(2). Posterior median plate of epigynum round, wider than lateral plates in posterior view (Fig. 124) .... *uzaga*
– Posterior median plate narrow, lateral plates wide (Figs. 136, 141) 4
4(3). In ventral view, epigynum length 1 to 1.5 width, tip at the point of an acute angle (Figs. 134, 135) .... *gavensis*
– In ventral view, epigynum wider than long, tip at the point of a shallow angle (Fig. 140) .... *iguape*
5(1). Thoracic region with at least a pair of macrosetae (Figs. 27, 32, 38) 6
– Thoracic region without macrosetae (Figs. 63, 80, 86) 17
6(5). Epigynum longer than wide in posterior view (Figs. 55, 151, 197) 7
– Epigynum wider than long to square in posterior view (Figs. 46, 50, 61) 9
7(6). In posterior view, median plate with a median constriction ventrally (top of Fig. 197); Amazon drainage, Peru (Map 4) .... *pakitza*
– Median plate entire (Figs. 151, 161) 8
8(7). In posterior view, dorsal swollen area of median plate triangular (bottom of Fig. 151); Peru (Map 4) .... *huanca*
– Dorsal, swollen area of median plate rectangular (Fig. 55); southern Venezuela (Map 4) .... *neblina*
9(6). In ventral view, epigynum with anterior pocket (Fig. 172); Bolivia to Mato Grosso, Brazil (Map 4) .... *yacuma*
– Epigynum without notch 10



Map 2. The number of species of *Wagneriana* in different areas.

10(9). In posterior view, median plate of epigynum with lateral, ventral constriction (top of Fig. 73); Espírito Santo State to Rio Grande do Sul, Brazil (Map 3) .... *taim*
– Posterior median plate without such constriction (Fig. 68) 11
11(10). Epigynum in ventral view framed on each side by lateral lobes (Fig. 67); in posterior view, median plate consisting of two round lobes (Fig. 68); Panama to Venezuela, Colombia (Map 3) .... *taboga*
– Epigynum in ventral view not framed; median plate without lobes 12
12(11). In posterior view, median plate narrow dorsally; posterior border to soft area less than half width of median plate (bottom of Figs. 25, 36, 46) 13
– Median plate wide dorsally (bottom of Fig. 41) 15
13(12). Median plate heart-shaped (Fig. 36); Venezuela, Guianas, Amazon drainage (Map 3) .... *jelskii*
– Posterior median plate otherwise (Figs. 25, 46) 14
14(13). In posterior view, dorsal area of median plate swollen and set off (bottom of Fig. 25); Panama to Amazon drainage (Map 3) .... *undecimtuberculata*
– Dorsal area of posterior median plate flat (Fig. 46); Peru (Map 3) .... *bamba*
15(12). In ventral view, base of epigynum forms acute angle (Fig. 40); in posterior view, posterior median plate ventral margin almost straight (top of Fig. 41); Guian-



Map 3. Distribution of *Wagneriana* species.

as, Amazon drainage to central Argentina (Map 3) .... *transitoria*

– Base of epigynum rounded (Figs. 29, 49); median posterior plate dorsally swollen (Figs. 30, 50) 16

16(15). In posterior view, posterior median plate narrower dorsally than ventrally (Fig. 50); Amazon drainage (Map 3) .... *jacaza*

– Posterior median plate swollen dorsally on each side (Fig. 30); Venezuela, Guianas, Peru, Amazon drainage (Map 3) .... *maseta*

17(5). Abdomen with anterior median projection (Figs. 203, 204); Venezuela (Map 4) .... *turrigera*

– Abdomen anteriorly rounded (Fig. 63) 18

18(17). Abdomen with only one pair of lateral tubercles enlarged (Figs. 63–66); Costa Rica, Pernambuco State, Brazil (Map 4) .... *grandicornis*

– Abdomen with most tubercles short or all extended (Figs. 108, 158) 19

19(18). Abdomen with most tubercles forming

long soft spines (Fig. 108); Minas Gerais State, Brazil, to central Argentina (Map 4) .... *heteracantha*
– Abdomen with most tubercles shorter (Figs. 158, 163) 20
20(19). Epigynum in posterior view longer than wide (Figs. 156, 161, 166) 21
– Epigynum in posterior view square to wider than long (Fig. 146) 24
21(20). In ventral view, base of epigynum with a neck (as in Figures 191, 192); ventral surface of head with a pair of dark marks (Fig. 191); southeastern U.S. to Venezuela and Ecuador (Map 4) .... *tauricornis*
– No such neck present (Figs. 156, 166) 22
22(21). In posterior view, median plate of epigynum round and containing median longitudinal groove (Fig. 156); Cuba, Hispaniola (Map 4) .... *vegas*
– Epigynum with median plate otherwise 23
23(22). In posterior view, median plate constricted in middle with a neck (Fig. 166); Colombia to Peru (Map 4) .... *tayos*
– Median plate with mid-ventral depression (Fig. 161); Guianas, Amazon drainage (Map 4) .... *acrosomoides*
24(21). In posterior view, median plate T-shaped (Fig. 146); Chaco, Paraguay (Map 4) .... *madrejon*
– Posterior median plate otherwise 25
25(24). In posterior view, median plate with a constriction (Figs. 178, 183, 188) 26
– Median plate without such constriction (Figs. 78, 111) 28
26(25). In ventral view, posterior margin of base of epigynum on each side of tip straight; no dark V-shaped mark (Fig. 187); Roraima Terr., Brazil (Map 4) .... *roraima*
– Posterior margin of epigynum in ventral view rounded; epigynum with V-shaped dark mark ventrally (Figs. 177, 182) 27
27(26). In posterior view, constriction of posterior median plate narrow (Fig. 178); Guianas, lower Amazon (Map 4) .... *hassleri*
– Constriction of posterior median plate wide (Fig. 183); upper Amazon (Map 4) .... *silvae*
28(25). In ventral view, epigynum base oval and set off in ventral view (Fig. 77); posterior view as in Figure 78; Rio de Janeiro, São Paulo States, Brazil (Map 3) .... *janeiro*
– Epigynum not set off anteriorly in ventral view (Figs. 110, 116) 29
29(28). In posterior view, lateral plates wider than median plate (Figs. 111, 117) 30
– Posterior median plate wider than lateral plates (Figs. 84, 94, 99) 31
30(29). Abdomen usually with narrow tail (Fig. 119); Trinidad to northern Argentina (Map 4) .... *neglecta*
– Abdomen usually short (Fig. 113); São Paulo State to Rio Grande do Sul, Brazil, Paraguay (Map 4) .... *eupalaestris*
31(29). In posterior view, median plate with wide transverse groove (Fig. 94); Costa Rica to southern Brazil (Map 3) .... *atuna*
– Posterior plate without such groove (Figs. 84, 99) 32
32(31). Posterior median plate with rounded ventral lateral lobes (Figs. 84, 85); northern Colombia, western Venezuela (Map 3) .... *cobella*
– Posterior plate without such lobes 33
33(32). In posterior view, median plate with dark septum above tip (top of Fig. 99) and posterior median plate round (Fig. 99); posterior margins in ventral view forming acute angle (Fig. 98); São Paulo State to central Argentina (Map 3) .... *juquia*
– No such dark septum; posterior plate rectangular (Fig. 89); posterior margin of base of epigynum almost straight (Fig. 88); Amazon area of Ecuador, Peru to Espírito Santo State, Brazil (Map 3) .... *lechuza*

KEY TO MALE *WAGNERIANA*

1. Anterior lateral tubercle of abdomen bifid (Fig. 128) 2
– Anterior lateral tubercle of abdomen simple or indistinct (Fig. 171) 5
2(1). Mexico to Costa Rica (Map 4) palpus as in Figure 133 .... *spicata*
– Southeastern Brazil to Paraguay 3
3(2). Median apophysis with thumb-shaped projection (Fig. 139) .... *gavensis*
– Median apophysis without such projection (Figs. 127, 144) 4
4(3). Terminal apophysis and conductor projecting above tegulum (Figs. 127, 144) .... *iguape*
– Terminal apophysis and conductor surrounded by tegulum (Fig. 127) .... *uzaga*
5(1). Embolus long and filiform (Figs. 170, 181) 6
– Embolus not filiform (Figs. 121, 127) 9
6(5). Embolus with loop (Figs. 170, 186) 7
– Embolus almost straight (Figs. 176, 181) 8
7(6). Median apophysis distally pointed as in Figure 186; upper Amazon (Map 4) .... *silvae*
– Median apophysis distally rounded as in Figure 170; Colombia to Peru (Map 4) .... *tayos*
8(6). Median apophysis with tooth and short

keel (Fig. 176). Misiones Prov., Argentina (Map 4) ..... *eldorado*

– Median apophysis with diagonal keel (Fig. 181); Guianas, lower Amazon (Map 4) ..... *hassleri*

9(5). Embolus a gently curved prong, its length almost half the diameter of palpus bulb (Fig. 44); Guianas, Amazon drainage to central Argentina (Map 3) ..... *transitoria*

– Embolus not a long, gently curved prong (Figs. 71, 164) 10

10(9). Conductor almost as large as median apophysis, visible diameters about equal (Fig. 164); Guianas, Amazon drainage (Map 4) ..... *acrosomoides*

– Conductor otherwise (Figs. 71, 102, 195) 11

11(10). A sclerotized filament (a part of terminal apophysis) hanging over distal edge of tegulum (Fig. 71); Panama, Venezuela, Colombia (Map 3) ..... *taboga*

– No such filament hanging over distal edge of tegulum (Figs. 102, 195) 12

12(11). Median apophysis with groove or split parallel to its long axis (Figs. 102, 195) 13

– Median apophysis without such split (Fig. 159) 14

13(12). Long axis of median apophysis parallel to that of cymbium (Fig. 195); southeastern U.S. to Venezuela and Ecuador ..... *tauricornis*

– Long axis of median apophysis at right angle to that of cymbium (Fig. 102); upper Amazon drainage (Map 3) ..... *carimagua*

14(12). Cuba, Hispaniola; palpus as in Figure 159 ..... *vegas*

– Central and South America 15

15(14). Median apophysis distally truncate as in Figures 114, 121 16

– Median apophysis of different shape (Fig. 92) 17

16(15). Truncate end of median apophysis round (Fig. 121); Trinidad to northern Argentina (Map 4) ..... *neglecta*

– Truncate end of median apophysis trapezoidal (Fig. 114); São Paulo to Rio Grande do Sul States, Brazil, Paraguay (Map 4) ..... *eupalaestris*

17(15). Median apophysis distally rounded and with two large teeth, one in front of other (Fig. 92); Amazon drainage area of Ecuador, Peru to Espírito Santo State, Brazil (Map 3) ..... *lechuza*

– Median apophysis otherwise (Fig. 154) 18

18(17). Conductor almost circular, covering embolus (Fig. 154); Bahia State, Brazil (Map 4) ..... *alma*

– Conductor longer than wide or square 19

19(18). Terminal apophysis in shape of half a wheel (Fig. 97); Costa Rica to southern Brazil (Map 3) ..... *atuna*

– Terminal apophysis otherwise 20

20(19). Base of embolus hidden by a flap from conductor and median apophysis with longitudinal and transverse keels (Fig. 28); Panama to Amazon drainage (Map 3) ..... *undecimtuberculata*

– Embolus and median apophysis otherwise (Figs. 34, 76) 21

21(20). Median apophysis with a tooth in middle (Figs. 34, 76) 22

– Median apophysis otherwise 23

22(21). Median apophysis with tooth and several other points (Fig. 34); Venezuela, Guianas, Peru, Amazon drainage (Map 3) ..... *maseta*

– Median apophysis with tooth and lobes (Fig. 76); Espírito Santo to Rio Grande do Sul States, Brazil (Map 3) ..... *taim*

23(21). Median apophysis with distal end folded forming a right angle as in Figure 87 or Figure 103 24

– Median apophysis with distal end otherwise 25

24(23). Median apophysis short with tubercle on "lower" margin (Fig. 87); northern Colombia, western Venezuela (Map 3) ..... *cobella*

– Median apophysis long, without tubercle (Fig. 103); Buenos Aires Prov., Argentina ..... *uropygialis*

25(23). Median apophysis with "vertical" keel in middle as in Figure 109; Minas Gerais State, Brazil, to central Argentina (Map 4) ..... *heteracantha*

– Median apophysis otherwise (Figs. 39, 53, 58, 81) 26

26(25). Median apophysis with rounded lobes as in Figure 39; Venezuela, Guianas, Amazon drainage (Map 3) ..... *jelskii*

– Median apophysis otherwise 27

27(26). Tegulum with knob distally (Fig. 81); Rio de Janeiro, São Paulo States, Brazil (Map 3) ..... *janeiro*

– Tegulum without such knob 28

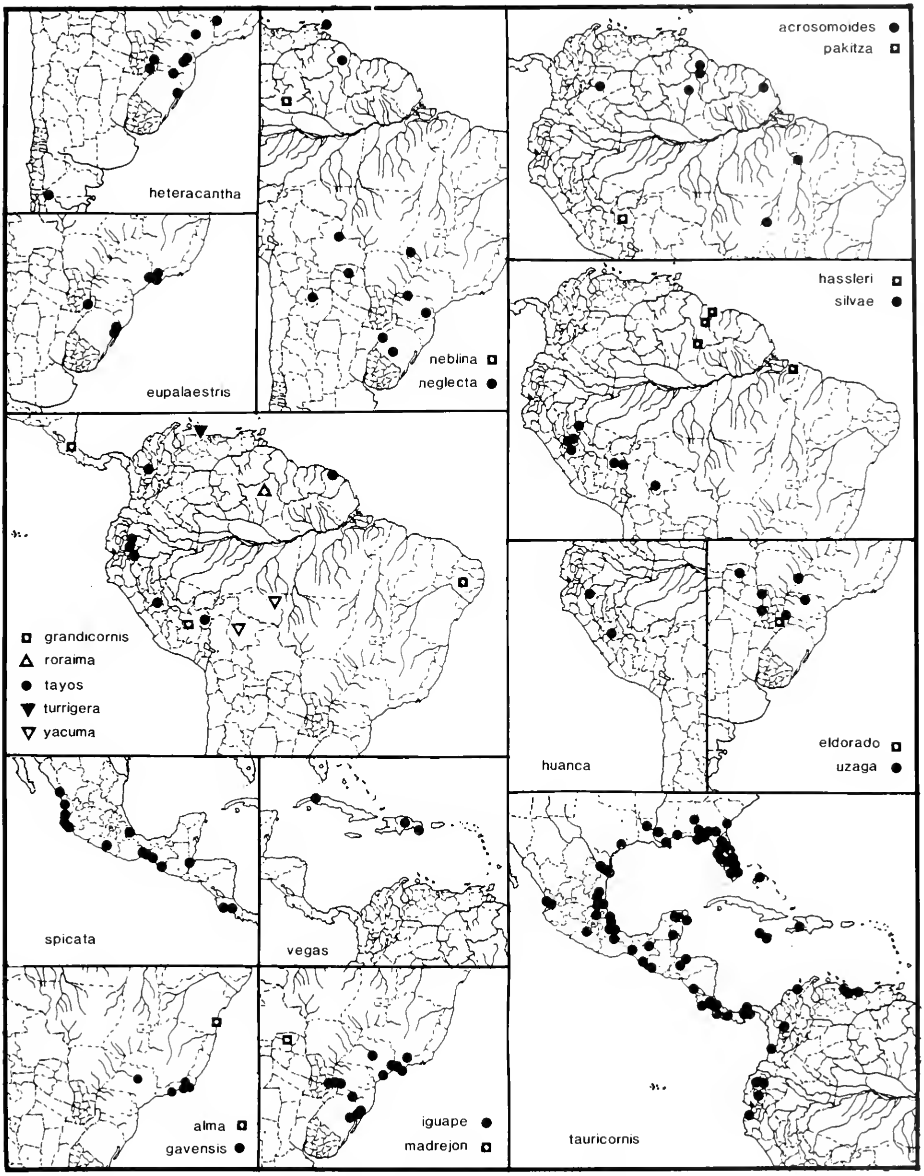
28(27). Embolus truncate (Fig. 53); Guatemala ..... *carinata*

– Embolus pointed (Fig. 58); southern Venezuela (Map 4) ..... *neblina*

Wagneriana undecimtuberculata (Keyserling)

Figures 24–28; Map 3

Epeira undecimtuberculata Keyserling, 1865: 805, pl. 18, figs. 1, 2, ♀, ♂. Female lectotype here designated from New Granada [historical name for



Map 4. Distribution of *Wagneriana* species.

Colombia and Panama], in BMNH, examined. Keyserling, 1892: 92, pl. 4, fig. 69, ♀, ♂.

Acrosoma tumida Taczanowski, 1879: 120, pl. 1, fig. 34, ♀. Female holotype from Amable María, [Depto. Junín], Peru, in PAN, examined. First synonymized by Levi, 1985.

Wagneriana undecimtuberculata:—F. P.-Cambridge, 1904: 498, pl. 47, figs. 17, 18, ♀, ♂. Roewer, 1942: 880. Bonnet, 1959: 4803.

Aranea tumida:—Roewer, 1942: 854.

Araneus tumidus:—Bonnet, 1955: 620.

Description. Female from Panama. Carapace orange to dark brown. Legs

ringed orange and brown. Venter of abdomen with two light patches. Carapace with two macrosetae (Fig. 27). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.5 diameters apart. Abdomen with 9 to 11 tubercles (Fig. 27). Total length 8.7 mm. Carapace 3.9 mm long, 2.9 mm wide. First femur 4.1 mm; patella and tibia 4.9 mm; metatarsus 2.4 mm; tarsus 1.1 mm. Second patella and tibia 4.2 mm; third, 2.3 mm; fourth, 3.5 mm.

Male from Panama. Color as in female. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes 1.1 diameters apart. Fourth trochanter with a thick, short macroseta. Total length 7.2 mm. Carapace 3.6 mm long, 2.7 mm wide. First femur 3.1 mm; patella and tibia 3.4 mm; metatarsus 2.1 mm; tarsus 0.8 mm. Second patella and tibia 3.2 mm; third, 2.0 mm; fourth, 2.9 mm.

Variation. The specimens illustrated came from Panama. Total length of females 7.2 to 11.7 mm, of males 6.2 to 7.4.

Diagnosis. In posterior view the epigynum differs from those of *W. spinosa* and *W. transitoria* by having the median dorsal area swollen and narrow (bottom of Fig. 25), while in *W. maseta* (Fig. 30) and *W. transitoria* (Fig. 41) it is wide, and in *W. jelskii* (Fig. 36) it is narrow and not swollen. The male differs in the sculpturing of the median apophysis, which has a proximal "vertical" keel and a median "horizontal" keel, together forming a T on its side (Fig. 28).

Natural History. Specimens have been found in a rain forest in Panama, on an oil palm in central Colombia, around a house in a suburb of Cali, in a banana plantation in a vertical orb web, and in a disturbed area in Ecuador.

Distribution. Panama, Amazonas State of Brazil, to eastern Peru (Map 3).

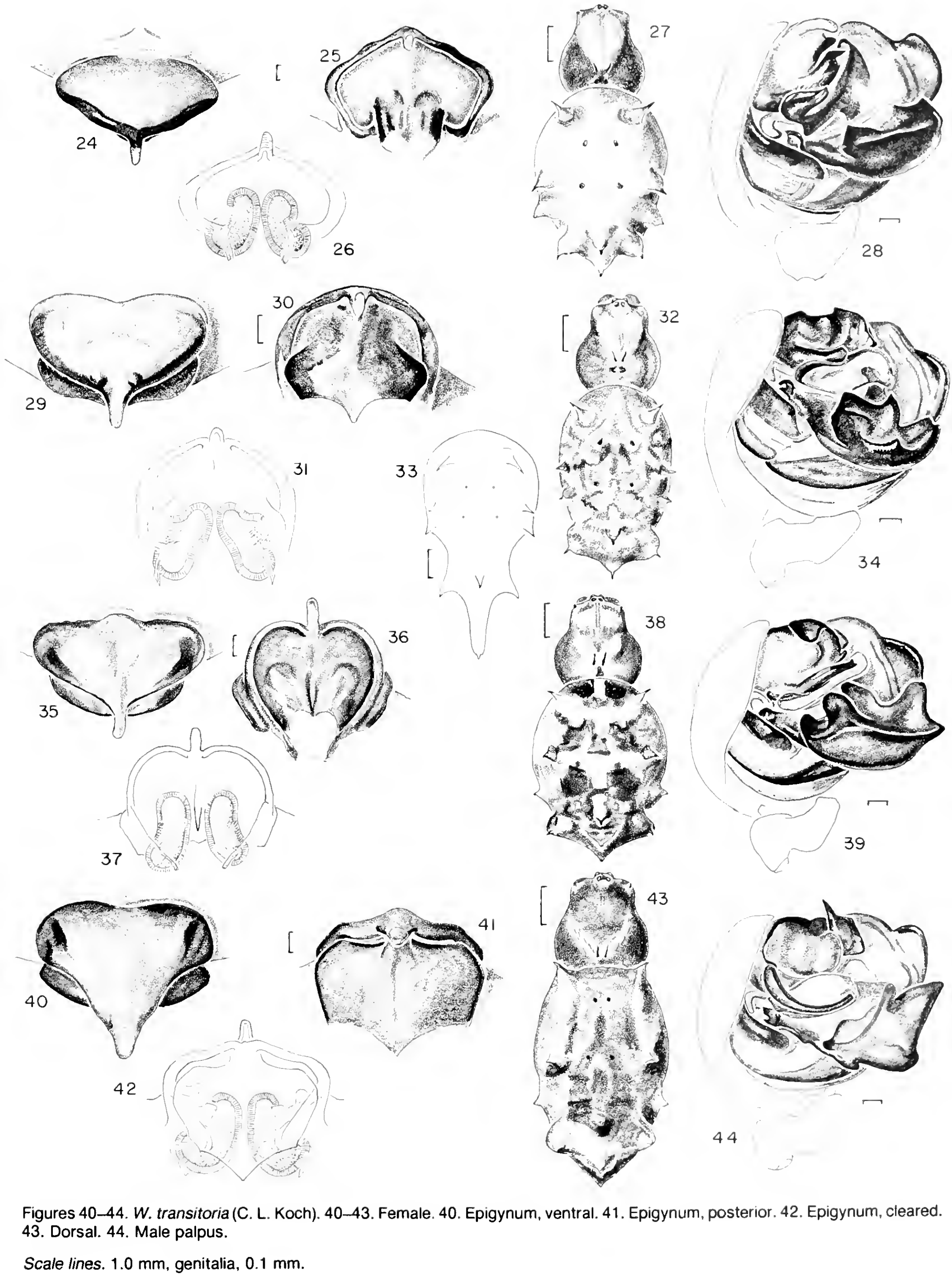
Records. PANAMA *Chiriquí:* David, ♀ (AMNH, MCZ); Bugaba, ♀ (MIUP). *Panamá:* Canal area, ♀, ♂, very common (AMNH, MCZ). TRINIDAD Port of Spain, ♀, ♂ (AMNH, MCZ); Arima, ♀ (AMNH). VENEZUELA *Aragua:* Rancho Grande, ♀ (AMNH). *Tachira:* Res. Forestal, ♀ (MCZ). COLOMBIA *Bolívar:* Cartagena, ♀ (MCZ). *Santander:* Río Opón, 1,000 m, ♀ (AMNH); Río Suárez, 800–1,000 m, ♀ (AMNH). *Cundinamarca:* nr. Sasaima, ♀ (DU). *Antioquia:* Turbo, ♀ (MCZ); Mutatá, ♀, ♂ (MCZ). *Chocó:* 20 km N Palestina, Río San Juán, ♀ (AMNH). *Meta:* 5km W Villavicencio, 820 m, ♀, ♂ (CAS); Villavicencio, ♀ (AMNH); Restrepo, ♀ (MCZ). *Valle:* 5 km W Delfina, 400 m, ♂ (AMNH); Cali, 1,000 m, ♀, ♂ (MCZ); Río Tuluá, 1,100 m, ♀ (MCZ); Guapi, 100 m, ♀ (MCZ). *Putumayo:* nr. Pto. Asis, Río Putumayo, ♀ (MCZ); *Caquetá:* Río Orteguaza, ♀ (AMNH). ECUADOR *Esmeraldas:* 11 km SE San Lorenzo La Chiquita, 5 m, ♀ (MCZ). *Napo:* Coca, Río Napo, ♀ (MCZ); Cuyabeno, Tarapoa, ♀ (MCZ). *Morona-Santiago:* Los Tayos, 05°70'S, 57°50'W, ♀ (MCZ). PERU *Huánuco:* Monsón Valley, Tingo María, 2♀ (CAS); Cucharas, 2♀ (CAS). Cueva de las Lechuza, Tingo María, ♀, ♂ (AMNH); Tingo María, ♀, ♂ (AMNH, CAS, MHNSM); Dantas-La Molina, SW Puerto Inca, 09°38'S, 75°00'W, ♀ (MHNSM). *Madre de Dios:* Estiron, Río Carbón, ♀ (MHNSM); Atacaya, Río Carbón, ♀ (MHNSM). BRAZIL *Amazonas:* Tefé, ♀ (MCZ); Igarape Belém nr. confluence Rio Solimões, ♀

→

Figures 24–28. *Wagneriana undecimtuberculata* (Keyserling). 24–27. Female. 24. Epigynum, ventral. 25. Epigynum, posterior. 26. Epigynum, cleared. 27. Dorsal. 28. Male left palpus.

Figures 29–34. *W. maseta* n. sp. 29–33. Female. 29. Epigynum, ventral. 30. Epigynum, posterior. 31. Epigynum, cleared. 32. Dorsal. 33. Abdomen, dorsal. 34. Male palpus.

Figures 35–39. *W. jelskii* n. sp. 35–38. Female. 35. Epigynum, ventral. 36. Epigynum, posterior. 37. Epigynum, cleared. 38. Dorsal. 39. Male palpus.



Figures 40–44. *W. transitoria* (C. L. Koch). 40–43. Female. 40. Epigynum, ventral. 41. Epigynum, posterior. 42. Epigynum, cleared. 43. Dorsal. 44. Male palpus.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

(AMNH); Hyutanahã, Rio Purus, ♀ (NRMS). *Rôndonia:* Porto Velho, ♀ (AMNH).

Wagneriana maseta new species
Figures 29–34; Map 3

Holotype. Male holotype with one female paratype from near Hacienda Mozambique, about 15 km N of Puerto Lopez, Depto. Meta, Colombia, 500 m, Aug. 1978 (W. Eberhard), in MCZ.

Description. Female paratype from Puerto Lopez, Colombia. Carapace orange to brown-black. Legs yellow ringed brown-black. Venter of abdomen blackish. Carapace with two macrosetae (Fig. 32). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 1.1 diameters apart. Abdomen with 11 tubercles (Figs. 32, 33). Total length 9.4 mm. Carapace 3.2 mm long, 2.5 mm wide. First femur 3.5 mm; patella and tibia 4.2 mm; metatarsus 2.1 mm; tarsus 0.9 mm. Second patella and tibia 3.5 mm; third, 2.0 mm; fourth, 3.0 mm.

Male holotype. Color as in female. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes 1.1 diameters apart. Fourth trochanter with two short macrosetae. Abdomen as in female. Total length 8.3 mm. Carapace 3.6 mm long, 2.7 mm wide. First femur 4.0 mm; patella and tibia 4.7 mm; metatarsus 2.4 mm; tarsus 0.9 mm. Second patella and tibia 3.4 mm; third, 2.2 mm; fourth, 3.1 mm.

Illustrations. The illustrations were made from the male holotype and female paratypes from Puerto Lopez.

Variation. Total length of females 8.2 to 11 mm, of males 7.1 to 8.3.

Diagnosis. In ventral view, the epigynum is more rounded behind (Fig. 29) than that of *W. transitoria* (Fig. 40) and, in posterior view, the median plate has bulges dorsally on the sides (bottom of Fig. 30) with a low area ventrally. The palpus differs from *W. jelskii* and *W. transitoria* by the shape of the short embolus, the large conductor, supporting the embolus, and the many-pointed median apophysis (Fig. 34).

Natural History. Specimens were collected in a savanna by tree fogging, in Guarico, Venezuela, and from wasp nests near Manaus, Brazil.

Distribution. Venezuela, Guianas, Colombia, Amazon area south to Ecuador (Map 3).

Paratypes. VENEZUELA *Terr. Delta Amacuro:* Río Orinoco delta, Jan., Feb. 1935, ♂ (N. Weber, MCZ). *Guarico:* Hato Masaquaral, 45 km S Calabozo, 17 Nov. 1980, ♂ (K. Rabenoid, MCZ). GUYANA *Bartica:* Kartabo, 1924, 2♀ (AMNH). SURINAM *Saramacca:* Voltzberg-Raleighvallen Nature Reserve, Feb. 1982, ♀ (D. Smith, MCZ). COLOMBIA *Meta:* Puerto Lleras, 14 July 1985, ♀ (B. Carroll, MCZ); Hacienda Mozambique, ca. 15 km SW Puerto Lopez, 200 m, July, Aug. 1978, 9♀, 2♂ (W. Eberhard, 1666, 1682, 1698, 1715, 1716, 1781, 1809, WS44, MOZ 1, MCZ). *Caquetá:* Río Orteguaza, Aug.–Sept. 1947, ♀ (L. Richter, AMNH). ECUADOR *Pichincha:* Río Palenque, km 47 on Santo Domingo-Quevedo Road, 150 m, 15 Mar. 1982, ♀, ♂ (Y. Lubin, YDL 383, MCZ). BRAZIL *Roraima:* Ilha de Maracá, 25 July 1987, ♀ (A. A. Lise, MCN 19656). *Amazonas:* Manaus, 2♀ (M.V. Bastos Garcia, INPA). *Pará:* Belém, Aug. 1971, ♀ (M. E. Galiano, MEG); Ligação Pará-Belém, km 305, ♀ (E. Dente, MZSP 7711).

Wagneriana jelskii (Taczanowski), new combination
Figures 35–39; Map 3

Epeira jelskii Taczanowski, 1873: 139. Male lectotype here designated from Cayenne, French Guiana, in PAN, examined (not female paralectotype).

Note. The female paralectotype of *W. jelskii* is *W. transitorium.* Simon (1895: 818), though he probably did not examine specimens, synonymized the name *W. jelskii* with *W. transitorium.* The male par-

alectotype (here designated) of *Epeira velutina* Taczanowski (1878: 159) from Amable María, Depto. Junín, Peru, is also *W. jelskii*. The lectotype and other paralectotypes of *E. velutina* belong to *Parawixia*. The type series of both *Epeira jelskii* and *Epeira velutina* were collected by wasps who did not distinguish between the species. They were harvested from wasp nests by the collector K. Jelski.

Description. Female from Browns Berg, Surinam. Carapace orange and dark brown with white setae. Legs yellowish with brown rings. Venter gray with two white patches. Carapace with two macrosetae (Fig. 38). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles (Fig. 38). Total length 8.7 mm. Carapace 3.1 mm long, 2.7 mm wide. First femur 3.9 mm; patella and tibia 4.5 mm; metatarsus 2.3 mm; tarsus 1.1 mm. Second patella and tibia 3.7 mm; third 2.1 mm; fourth, 3.4 mm.

Male from Ikurua River, Guyana. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with one short macroseta. Total length 8.3 mm. Carapace 3.5 mm long, 2.5 mm wide. First femur 3.8 mm; patella and tibia 4.5 mm; metatarsus 2.5 mm; tarsus 0.9 mm. Second patella and tibia 3.1 mm; third, 2.1 mm; fourth, 2.8 mm.

Illustration. The illustrations were made from a female from Browns Berg, Surinam, and a male from Ikurua River, Guyana.

Note. The match of male with female is uncertain although male and female were collected at the same locality in Bolivia.

Variation. Total length of females 8.2 to 10.7 mm, of males 7.6 to 8.3.

Diagnosis. The female differs from *W. undecimtuberculata* by the heart-shaped posterior median plate of the epigynum, with its dorsal margin (bottom of Fig. 36) not raised. The male differs by lacking the proximal sclerotized lobe of the conductor of the palpus present in related species, and by having a distal lobe on the median apophysis (Fig. 39).

Natural History. The male from Guyana was collected in a forest savanna, the male from Bolivia in a high forest. Both the females from Bolivia were collected at night. The specimens from Manaus, Brazil, came from a wasp nest.

Distribution. Trinidad, northern Venezuela, Amazon drainage (Map 3).

Records. LESSER ANTILLES *Trinidad:* Piarco, 27 Nov. 1954, ♂ (A. M. Nadler, AMNH). VENEZUELA *Tachira:* Reserva Forestal, 9 Sept. 1977, ♀ (Y. Lubin, MCZ). *Monagas:* Caripito, 16–30 Apr. 1942, ♀ (W. Beebe, AMNH). *Carabobo:* San Esteban, Dec. 1891, ♀ (Meinert, ZMK). *Dto. Federal:* Caracas, Sept. 1891, ♀ (Meinert, ZMK). GUYANA Canje, Ikurua Rivers, 5°70'N, 57°50'W, Aug.–Dec. 1961, ♂ (G. Bentley, AMNH). SURINAM *Brokopondo Prov.:* Browns Berg, 20 Feb. 1982, ♀ (D. Smith Trail, MCZ). ECUADOR *Napo:* Reserva Forestal Cuyabeno, 27 July 1985, ♀ (L. Avilés, MECN). PERU *Madre de Díos:* Zona Reservada Tambopata, 23–26 May 1987, 22 July 1987, 9 June 1988, 3♀ (D. Silva D., MHNSM). BRAZIL *Roraima:* Ilha de Maracá, 20 July 1987, ♀ (A. A. Lise, MCN). *Amapá:* Vila Amazonas [?], 21 Mar. 1964, ♀ (C. E., E. S. Ross, CAS). *Amazonas:* Reserva Ducke, Manaus, 24 Mar. 1964, ♀ (C. E., E. S. Ross, CAS); Manaus, 2♀, ♂ (M.V. Bastos Garcia, INPA). BOLIVIA *Cochabamba:* Zischka's Camp, nr. San Antonio, Río Chipiriri, Oct., Nov. 1953, ♀ (W. Forster, O. Schindler, ZSM). *Beni:* Estac. Biol. Beni, 9 Sept. 1987, 2♀, 8–14 Sept. 1987, ♂ (J. Coddington, S. Larcher, USNM).

Wagneriana transitoria (C. L. Koch)
Figures 40–44; Map 3

Acrosoma transitorium C. L. Koch, 1839: 119, pl. 208, fig. 518, ♀. Female holotype from Brazil, in ZSM, destroyed during World War II.

Epeira spinosa Taczanowski, 1873: 141, pl. 5, fig. 18,

♀. Female lectotype from St. Laurent du Maroni, French Guiana, in PAN, here designated. First synonymized by Simon, 1895.

Araneus transitorius:—Simon, 1895: 818.

Edricus transitorius:—Petrunkevitch, 1911: 338. Bonnet, 1956: 1648.

Anawixia atopa Chamberlin, 1916: 258, pl. 20, figs. 1–3, ♂. Male holotype from San Miguel, 6,000 ft [1,800 m], Depto. Ayacucho, Peru, in MCZ, examined. Roewer, 1942: 778. Bonnet, 1955: 315. NEW SYNONYMY.

Aranea transitoria:—Roewer, 1942: 854.

[?] *Wagneriana vermiculosa* Mello-Leitão, 1949: 10, imm. Penultimate instar female holotype from Rio Holuene (Rio Coluene) confluence with Rio Xingu, Mato Grosso, Brazil, in MNRJ. DOUBTFUL NEW SYNONYMY.

Note. Although Koch's illustration is not diagnostic for species recognition, it seems reasonable to use his name, the oldest name for a Brazilian *Wagneriana* species having two macrosetae on the carapace, for the most common, widespread species. Taczanowski's lectotype of *E. spinosa* is in a vial with three immatures. Another female marked *spinosa* by Taczanowski from Cayenne may be *W. maseta*, but this is not certain.

Simon (1895) synonymized *Epeira jelskii* Taczanowski and *Epeira spinosa* Taczanowski with *transitoria*. A vial labeled *W. transitoria* was found in the Simon collection containing two females from "Muloui Portal" [?]; one was *W. jelskii* and the other *W. maseta*.

Description. Female from Dpto. Huánuco, Peru. Carapace dark brown to orange with white setae. Legs yellowish with irregular black rings. Venter of abdomen black with some white pigment under transparent integument, black on sides and posterior of center. Carapace with two macrosetae (Fig. 43). Posterior median eyes same diameter as anterior medians, laterals 0.9 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles (Fig. 43). Total length 8.8 mm. Carapace 3.8 mm long, 2.7 mm wide. First femur 3.9 mm; patella and tibia 4.6 mm; metatarsus 2.4 mm; tarsus 0.9 mm. Second patella and tibia 3.8 mm; third, 2.1 mm; fourth, 3.4 mm.

Male holotype of *A. atopa*. Cephalic region orange, thoracic region brown. Legs orange with brown rings. Abdomen dusky. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes 1.2 diameters apart. Fourth trochanter with one short macroseta. Total length 7.0 mm. Carapace 3.4 mm long, 2.5 mm wide. First femur 4.1 mm; patella and tibia 4.3 mm; metatarsus 2.4 mm; tarsus 1.0 mm. Second patella and tibia 3.1 mm; third, 2.1 mm; fourth, 2.9 mm.

Illustrations. The female illustrated came from Depto. Huánuco, Peru; the male is the holotype of *A. atopa*.

Variation. Total length of females 5.6 to 9.6 mm, of males 4.8 to 8.1. One female from Bolivia lacked the characteristic macrosetae on the carapace. Many females have more than two setae on the carapace. The outline of the characteristic acute tip of the epigynum in ventral view is variable.

Diagnosis. The epigynum can be separated from those of *W. maseta* and *W. jelskii* (Figs. 29, 35) by the acute angle formed by the tip in ventral view (Fig. 40) and by the shape of the posterior median plate in ventral view and narrow lateral plates in posterior view (top of Fig. 41). The male can be separated from related species by the gently curved embolus positioned at a right angle close to the edge of the cymbium and the shape of the median apophysis, which has a longitudinal curved keel ending in a small basal knob (Fig. 44).

Natural History. Some specimens have been taken from wasp nests. Females came from a cerrado shrub from Mato Grosso State, Brazil.

Distribution. Venezuela, Amazon drainage, to southern Argentina (Map 3).

Records. VENEZUELA *Bolívar:* Río Caura, Campamento Cecilia Magdalena (CAS). GUYANA Kartabo (CUC, AMNH); Tumatumari (AMNH). SURINAM *Saramacca:* Voltzberg (MCZ). *Marouwijne:* Lawa River, Anapaike Village (AMNH).

FRENCH GUIANA nr. Cayenne (MCZ). COLOMBIA *Caquetá:* Río Orteguaza, 200 m (AMNH). *Cundinamarca:* "Cosomoco, 800 m" [Susumuco], (NHMW). *Amazonas:* 8–16 km W Leticia (MPM). ECUADOR *Napo:* Bridge over Río Cuyabeno (MCZ). *Pastaza:* Montalvo (MECN). PERU *Loreto:* Indiana (MHNSM). *Pasco:* Río Iscozacin (MHNSM); Pan de Azúcar [?], (AMNH). *San Martín:* Rio Huallaga, Saposoa, 424 m, (CAS). *Ucayali:* Pucallpa (AMNH). *Huánuco:* Divisoria, 1,700 m (AMNH); Boquerón del Padre Abad (MHNSM); Cuevas de las Lechuza, Tingo María (AMNH). *Junín:* Utcuyacu, 1,600–2,200 m (AMNH). BRAZIL *Amapá:* Serra do Navio (MEG). *Roraima:* Ouro Prêto do Oeste (MNRJ). *Pará:* Aldeia, Aracu, Gurupi-Uma, 50 km E Canindé (AMNH); Rio Gurupi (AMNH, MZSP 3299, 3368); 30 km S Belém (CAS); Belém (MCZ, MEG); Jacará-Acanga (AMNH). *Amazonas:* Tefé (MCZ); Reserva Ducke, Manaus (CAS, MCN); Manaus, (MEG, INPA, MZSP 1899, 3010, NRMS); km 62 Manaus to Caracaraí (MCN 9484); Chicago, Rio Japurá (NRMS); Rio Negro, Umarituba (NRMS). *Alagoas:* Mangabeiras (MZSP 8291). *Bahia:* Fazenda Escalvada, Mucuri (MCN 11105). *Mato Grosso:* 260 km N Xavantina, 400 m (MCZ); Xingu Culuene (MNRJ); Utiariti (K. Lenko, MZSP 5626); Barra dos Bugres (MNRJ); Barra do Tapirapé (AMNH, MZSP 3383, 3401); Chapada dos Guimarães (MCN 12329). *Mato Grosso do Sul:* Três Lagoas (MZSP 3669). *Minas Gerais:* Pedra Azul (AMNH). *São Paulo:* Botucatu (IMPR); Mata do Procopua, Porto Ferreira (MZSP 6446). *Paraná:* Rôlandia (AMNH); Alto Paraná, Iaguararapa (AMNH). *Rio Grande do Sul:* Porto Garcia, Tenente Portela (MCN 4613); Garruchos, São Borja (MCN 8722, 8770); Salto do Yucuma, (MCN 12856, 12857). PARAGUAY *Alto Paraná:* km 12 de Stroessner, Centro Forestal de Alto Paraná (IBNP). BOLIVIA *La Paz:* Yungas de Palmas (ZSM). *Beni:* Estac. Beni, 5 km N El Porvenir (USNM); Cavinas (USNM). ARGENTINA *Misiones:* Eldorado (AMNH); Parque Nac. Iguazu (MEG); Montecarlo (MEG); Depto. San Antonio (MEG). *Río Negro:* El Bolsón (AMNH).

Wagneriana bamba new species
Figures 45–48; Map 3

Holotype. Female holotype from Huancabamba, Quebrada Castillo, NW of Iscozacin, 345 m, 10°10'S, 75°15'W, Pasco, Peru, 13 Sept. 1987 (D. Silva D.), in MHNSM. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange, sides of thoracic region dark brown. Legs orange to brown, indistinctly ringed. [Abdomen damaged.] Carapace with two macrosetae (Fig. 48). Posterior median eyes 0.9 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Abdomen with four pairs of lateral tubercles and three median posterior (Fig. 48). Total length 10 mm. Carapace 3.7 mm long, 2.7 mm wide. First femur 4.1 mm; patella and tibia 4.8 mm; metatarsus 2.5 mm; tarsus 1.1 mm. Second patella and tibia 4.0 mm; third, 2.3 mm; fourth, 3.5 mm.

Diagnosis. The shape of the posterior median plate of the epigynum, which is oval (Fig. 46), differs from that of *W. transitoria.* (Fig. 41).

Wagneriana jacaza new species
Figures 49–52; Map 3

Holotype. Female holotype from Jacareacanga, Pará State, Brazil, Oct. 1959 (M. Alvarenga), in AMNH. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange to dark brown with white setae. Legs orange with brown rings. Venter of abdomen with white V-shaped mark on light brown. Carapace with two macrosetae (Fig. 52). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles (Fig. 52). Total length 11.3 mm. Carapace 4.0 mm long, 2.9 mm wide. First femur 4.4 mm; patella and tibia 4.8 mm;

metatarsus 2.7 mm; tarsus 1.1 mm. Second patella and tibia 4.2 mm; third, 2.4 mm; fourth, 3.7 mm.

Illustration. The holotype was illustrated.

Note. W. carimagua might be the male of this species.

Diagnosis. In ventral view, the posterior margin of the epigynum is round (Fig. 49), and, in posterior view, the median plate is narrower dorsally than ventrally (Fig. 50).

Paratypes. BRAZIL *Amazonas:* Manaus, Canal de Janauari, 16–17 June 1987, ♀ (H. Höfer, INPA); Manaus, Ilha de Marchantaria, 15 Dec. 1987, ♀ (H. Höfer, INPA). *Mato Grosso:* Chavantina, Nov. 1946, ♀ (H. Sick, MZSP 1224); Barra do Tapirape, 1–5 Jan. 1961, ♀ (B. Malkin, AMNH).

Wagneriana carinata F. P.-Cambridge
Figure 53; Map 3

Wagneriana carinata F. P.-Cambridge, 1904: 498, pl. 47, fig. 16, ♂. Male holotype from Cobán, Guatemala, in BMNH, examined. Roewer, 1942: 880. Bonnet, 1959: 4803.

Araneus cacozelus Petrunkevitch, 1911: 283. New name for *W. carinata*, erroneously thought to be preoccupied by *Epeira carinata* Nicolet, 1849.

Description. Male holotype. Carapace brownish black, cephalic region yellowish. Legs yellowish. Venter of abdomen dusky underlain by white pigment spots, black on each side of petiole. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes slightly more than their diameter apart. Fourth trochanter with one short macroseta. Abdomen with 11 tubercles. Total length 6.0 mm. Carapace 2.7 mm long, 1.8 mm wide. First femur 3.1 mm; patella and tibia 3.5 mm; metatarsus 1.9 mm; tarsus 0.8 mm. Second patella and tibia 2.4 mm; third, 1.8 mm; fourth, 2.2 mm.

Note. A female in the vial with the male holotype is *W. tauricornis.* The female is not mentioned in the original description. No other specimens of *W. carinata* have been found.

Diagnosis. The median apophysis has a distinctive shape, its "lower" edge appears rolled up (Fig. 53).

Wagneriana neblina new species
Figures 54–59; Map 4

Holotype. Female holotype from Cerro de Neblina, base camp, 140 m, on low foliage, 0°50′N, 66°10′W, Territ. Fed. Amazonas, Venezuela, 21–28 Feb. 1985 (W. E. Steiner), in USNM. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace dusky orange-brown with some short white hair on cephalic region. Legs yellow with dark brown rings. Venter of abdomen with two white patches side by side. Carapace with three macrosetae (Fig. 57). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles (Fig. 57). Total length 9.8 mm. Carapace 3.6 mm long, 2.9 mm wide. First femur 4.2 mm; patella and tibia 5.0 mm; metatarsus 2.5 mm; tarsus 1.0 mm. Second patella and tibia 4.5 mm; third, 2.3 mm; fourth, 3.6 mm.

Male from type locality. Color as in female, but no rings on first two pairs of legs.

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Figures 45–48. *Wagneriana bamba* n. sp., female. 45. Epigynum, ventral. 46. Epigynum, posterior. 47. Epigynum, cleared. 48. Dorsal.

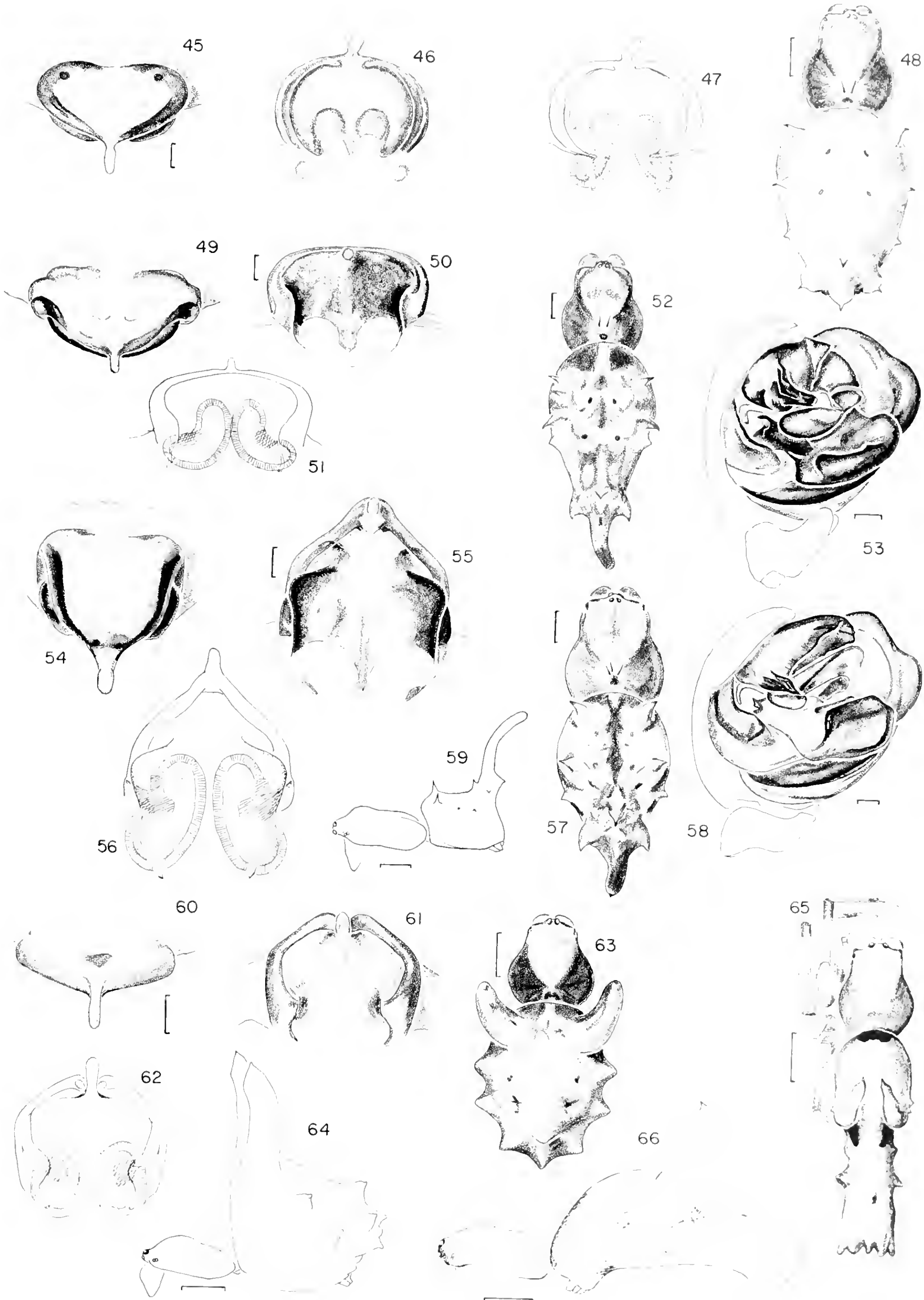
Figures 49–52. *W. jacaza* n. sp., female. 49. Epigynum, ventral. 50. Epigynum, posterior. 51. Epigynum, cleared. 52. Dorsal.

Figure 53. *W. carinata.* F. P.-Cambridge, male left palpus.

Figures 54–59. *W. neblina* n. sp. 54–57. Female. 54. Epigynum, ventral. 55. Epigynum, posterior. 56. Epigynum, cleared. 57. Dorsal. 58, 59. Male. 58. Palpus. 59. Lateral.

Figures 60–66. *W. grandicornis* (Mello-Leitão). 60–64. Female. 60. Epigynum, ventral. 61. Epigynum, posterior. 62. Epigynum, cleared. 63. Dorsal. 64. Lateral. 65, 66. Immature holotype. 65. Dorsal. 66. Lateral.

Scale lines. 1.0 mm, genitalia, 0.1 mm.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Posterior median eyes 0.6 diameter of anterior medians, laterals 0.4 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes slightly less than their diameter apart. Fourth trochanter with one short thick macroseta. Abdomen with ten tubercles and a long tubular tail (Fig. 59). Total length 7.5 mm. Carapace 3.0 mm long, 2.3 mm wide. First femur 3.4 mm; patella and tibia 3.4 mm; metatarsus 1.8 mm; tarsus 0.9 mm. Second patella and tibia 2.8 mm; third, 1.7 mm; fourth, 2.3 mm.

Diagnosis. The female differs from *W. maseta* by the longer than wide outline of the epigynum (Fig. 54). The male differs from others by the shape of the median apophysis (Fig. 58).

Natural History. Specimens were collected with a Malaise trap over a small stream.

Paratype. VENEZUELA *Amazonas:* type locality, 20–24 Mar. 1984, ♂ (O. Flint, J. Louton, USNM).

Wagneriana grandicornis Mello-Leitão
Figures 60–66; Map 4

Wagneriana grandicornis Mello-Leitão, 1935: 96, pl. 6, imm. Immature holotype from Pesqueira, Pernambuco, Brazil, in MNRJ, examined. Roewer, 1942: 880. Bonnet, 1959: 4803.

Description. Immature female holotype. Carapace brown, cephalic region yellowish. Clypeus with a brown band lying between lateral eyes on each side and touching posterior median eyes. Legs ringed brown. Venter with a black patch. Eyes facing forward. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes 1.5 diameters apart. Posterior median eyes 1.3 diameters apart. Abdomen with a pair of large, lateral projections and small tubercles (Figs. 65, 66). Total length 7.5 mm. Carapace 2.0 mm long, 1.5 mm wide. First femur 2.1 mm; patella and tibia 2.2 mm; metatarsus 1.0 mm; tarsus 0.5 mm. Second patella and tibia 2.0 mm; third, 1.2; fourth, 1.4 mm.

Note. The only adult that might belong to this species is a female found in Costa Rica (Figs. 60–64). Its abdomen is short (Figs. 63, 64), but probably within the variation of the species. Its measurements are total length 5.8 mm. Carapace 2.3 mm long, 1.8 mm wide. First femur 2.6 mm; patella and tibia 2.9 mm; metatarsus 1.4 mm; tarsus 0.7 mm. Second patella and tibia 2.5 mm; third, 1.3 mm; fourth, 2.1 mm. Figures 65, 66 were made from the holotype.

Diagnosis. This species differs from all others by having the most anterior lateral tubercles of the abdomen projecting dorsally (Figs. 63–66).

Records. COSTA RICA *Heredia:* La Selva, 4 km SE Puerto Viejo, from trap nest collection, prey of wasp *Trypoxylon lactitarse*, 29 July 1980, ♀ [uncertain if *W. grandicornis*], (R. E. Coville AR Ø9, MCZ).

Wagneriana taboga new species
Figures 67–71; Map 3

Holotype. Female holotype from Summit, Panamá Prov., Panama, July 1950 (A. M. Chickering), in MCZ. The specific name is a noun in apposition after a locality where the species is abundant.

Description. Female from Taboga Island. Carapace orange to brownish black. Legs orange with black patches. Venter of abdomen with a black square between epigynum and spinnerets. Carapace with two macrosetae (Fig. 70). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.2 diameters apart. Abdomen with 11 tubercles (Fig. 70). Total length 4.8 mm. Carapace 2.1 mm long, 1.5 mm wide. First femur 1.8 mm; patella and tibia 2.1 mm;

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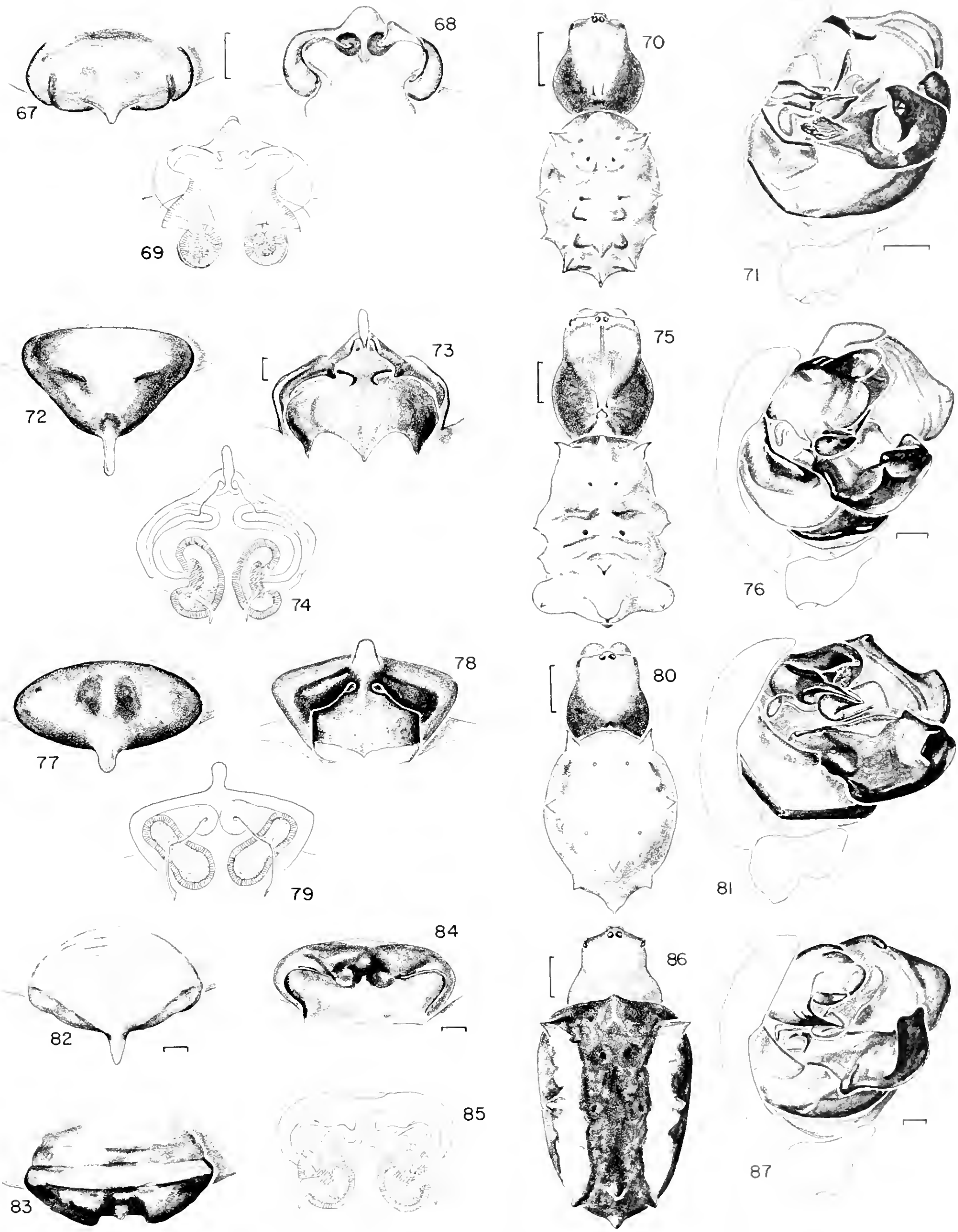
Figures 67–71. *Wagneriana taboga* n. sp. 67–70. Female. 67. Epigynum, ventral. 68. Epigynum, posterior. 69. Epigynum, cleared. 70. Dorsal. 71. Male left palpus.

Figures 72–76. *W. taim* n. sp. 72–75. Female. 72. Epigynum, ventral. 73. Epigynum, posterior. 74. Epigynum, cleared. 75. Dorsal. 76. Male palpus.



Figures 77–81. *W. janeiro* n. sp. 77–80. Female. 77. Epigynum, ventral. 78. Epigynum, posterior. 79. Epigynum, cleared. 80. Dorsal. 81. Male palpus.

Figures 82–87. *W. cobella* n. sp. 82–86. Female. 82, 83. Epigynum, ventral. 83. Scape torn off. 84. Epigynum, posterior. 85. Epigynum, cleared. 86. Dorsal. 87. Male palpus.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

metatarsus 1.3 mm; tarsus 0.5 mm. Second patella and tibia 1.8 mm; third, 1.1 mm; fourth, 1.8mm.

Male from Taboga Island. Color as in female. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with one short macroseta. Abdomen tubercles less distinct than those of female. Total length 3.9 mm. Carapace 2.1 mm long, 1.5 mm wide. First femur 2.1 mm; patella and tibia 2.3 mm; metatarsus 1.2 mm; tarsus 0.5 mm. Second patella and tibia 1.7 mm; third, 1.1 mm; fourth, 1.7 mm.

Illustration. The illustrations were made from specimens from Taboga Island.

Variation. The tip of the epigynum may be transparent (Fig. 67) or dark brown and sclerotized. Total length of females 4.7 to 6.5 mm, of males 3.6 to 4.2.

Diagnosis. The epigynum is relatively flat unlike that of other species (Fig. 67) and the posterior median plate has two lobes (Fig. 68). The male palpus differs from that of similar species by having a black sclerotized prong, part of the terminal apophysis, protruding from the distal edge of the tegulum (Fig. 71).

Natural History. Specimens have been collected in woods at night in Panama and from vegetation in the Depto. Magdalena, Colombia.

Distribution. Panama, western Venezuela, and Colombia (Map 3).

Paratypes. PANAMA *Colón:* Portobelo, Aug. 1939, 2♀, ♂ (A. M. Chickering, MCZ); Fuerte Davis, July 1936, ♂ (A. M. Chickering, MCZ); Fort Sherman, 3 July, ♀ (N. Banks, MCZ). *Panamá:* Forest Reserve, Aug. 1936, 2♂, 24 Dec. 1957, ♀ (A. M. Chickering, MCZ); Experimental Gardens, July, Aug. 1954, 2♀, 2♂ (A. M. Chickering, MCZ); Balboa, 17 Aug. 1936, ♀ (A. M. Chickering, MCZ); nr. Balboa, 28 Aug. 1946, ♀ (N. L. H. Krauss, AMNH); Fort Kobbe, 3 Aug. 1983, 4♀, ♂ (H. W. Levi, H. Stockwell, MCZ); Cocoli, Mar.–May 1954, ♀ (W. E. Lundy, AMNH); Taboga Isl., 29 June, ♂ (N. Banks, MCZ), Dec. 1953, ♀, 22 Aug. 1946, 2♀, ♂ (N. L. H. Krauss, AMNH); Barro Colorado Isl. June, July 1934, ♀, ♂ (A. M. Chickering, MIUP); Madden Dam, July 1950, ♀, ♂, 27 July 1954, ♂ (A. M. Chickering, MCZ, MIUP); Reserva Forestal, Madden, 15, 16 May 1977, 2♀, ♂ (D. Quintero, MIUP); Cerro Galera, July 1981, ♂, July 1985, 2♀, ♂ (W. Eberhard, MCZ); Pipeline Road, ♀ (FSCA). *Chiriquí:* David, 26 Nov. 1975, ♀ (D. Quintero, MIUP). VENEZUELA *Carabobo:* San Esteban, 21 Jan. 1940, ♀ (P. Andruze, CUC), 26 Jan. 1940, ♀ (P. Andruze, AMNH). COLOMBIA *Magdalena:* Bahia de Guairaca, Tayrona Park, 20 km E Santa Marta, 29 May 1985, ♂ (H.-G. Müller, SMF). *Bolivar:* Cartagena, 16 Feb. 1974, ♂ (A. B. Schneble, MCZ). *Cundinamarca:* Villetta, 800 m, 18 Sept. 1973, ♂ (A. B. Schneble, MCZ).

Wagneriana taim new species
Figures 72–76; Map 3

Holotype. Female holotype from Novo Hamburgo, Rio Grande do Sul State, Brazil, 4 Nov. 1985 (A. A. Lise), in MCN no. 14352. The specific name is a noun in apposition after the locality of the male paratype.

Description. Female holotype. Cephalic region yellowish, with a tranverse dark line behind eyes, line curved on each side (Fig. 75), thoracic region brown. Legs yellowish with brown rings. Venter brown with white spots under integument. Carapace with two macrosetae (Fig. 74). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes slightly more than their diameter apart. Abdomen with 11 tubercles (Fig. 75). Total length 8.2 mm. Carapace 3.5 mm long, 2.5 mm wide. First femur 3.8 mm; patella and tibia 4.6 mm; metatarsus 2.3 mm; tarsus 0.9 mm. Second patella and tibia 3.8 mm; third, 2.2 mm; fourth, 3.4 mm.

Male from Taim, Rio Grande do Sul, Brazil. Cephalic region yellowish, sides of carapace black , both covered with sparse, short, white setae. Legs yellowish with brown to black rings. Venter of abdomen

spotted dusky. Posterior median eyes same diameter as anterior medians, anterior laterals same diameter, posterior laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with one short macroseta. Abdomen with one small anterior pair of tubercles and four posterior pairs, and a median posterior tubercle. Total length 5.5 mm. Carapace 2.1 mm long, 1.7 mm wide. First femur 2.6 mm; patella and tibia 2.7 mm; metatarsus 1.4 mm; tarsus 0.7 mm. Second patella and tibia 2.0 mm; third, 1.3 mm; fourth, 1.8 mm.

Illustration. The female holotype is illustrated.

Note. It is uncertain that the male is conspecific.

Variation. Total length of females 9.2 to 12.0 mm. Some females lack carapace setae.

Diagnosis. The female is separated from others by the shape of the ventrally constricted posterior median plate in posterior view (top of Fig. 73); the male is separated by the presence of a long distal lobe of the tegulum, the drop-shaped embolus, and the shape of the median apophysis (Fig. 76).

Paratypes. BRAZIL *Bahia:* Itamaraju, Feb. 1985, ♀ (MNRJ). *Espírito Santo:* 12–27 Oct. 1962, ♀ (P. Pereira, MZSP 7678); Conceicão da Barra, ♀ (Ruschi, MNRJ); S. Francisco Xavier, Serra Mantigueira, Dec. 1944, ♀ (E. Denta, MZSP 7600). *Minas Gerais:* ♀ (NHMW); Rio Matipó, Aug. 3, ♀ (MZSP 5777). *Rio de Janeiro:* Teresópolis, 27 Sept. 1944, ♀ (P. Wygodzinsky, MZSP 9618); Itatiaia, 20 Feb. 1943, ♀ (P. Wygodzinsky, MZSP 5735). *São Paulo:* Boraceia, 12 Jan. 1961, ♀ (P. Biasi, MZSP 7725); Engenheiro Marcilac St. Amaro, 16–17 Dec. 1966, ♀ (P. Biasi, MZSP 5400); Caraguatatuba, May 1962, ♀ (MZSP 7944); Ilha de São Sebastião, 15–21 Jan. 1948, ♀; 24 Aug. 1967, ♀ (H. Urban, MZSP 7169, 7419). *Rio Grande do Sul:* Taim, 2 Sept. 1986, ♂ (C. J. Beener, MCN 15657); Irai, 20 Nov. 1975, ♀ (A. Lise, MCN 3132).

Wagneriana janeiro new species
Figures 77–81; Map 3

Holotype. Female holotype from Rio de Janeiro, Brazil, 26 May 1979 (C. J. Becker), in MCN no. 8582. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Cephalic region orange with some white setae, sides of thoracic region brown to black. Legs yellowish with brown rings. Venter of abdomen black between epigynum and spinnerets with a white line on each side of dark patch. Carapace without macrosetae. (Anterior median eyes absent from holotype only.) Lateral eyes 0.6 diameter of posterior median eyes. Posterior median eyes 1.2 diameters apart. Laterals separated by slightly less than their diameter. Abdomen with only eight tubercles (Fig. 80). Total length 5.8 mm. Carapace 2.3 mm long, 1.7 mm wide. First femur 2.2 mm; patella and tibia 2.7 mm; metatarsus 1.3 mm; tarsus 0.7 mm. Second patella and tibia 2.3 mm; third, 1.3 mm; fourth, 2.0 mm.

Male from Botucatu. Color as in female, but with a transverse dark patch on cephalic region. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with one short macroseta. Abdomen with about 11 tubercles. Total length 5.2 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.5 mm; patella and tibia 3.0 mm; metatarsus 1.7 mm; tarsus 0.7 mm. Second patella and tibia 2.3 mm; third, 1.3 mm; fourth, 2.1 mm.

Note. The male and the females were matched because they were collected at the same site. The female holotype has only six eyes, an abnormality. The lateral edge of the median apophysis differs slightly in the two males.

Illustration. The female holotype and the male from Botucatu were illustrated.

Variation. Total length of females 6.0 to 6.3 mm.

Diagnosis. The epigynum in ventral view is oval and set-off all around (Fig. 77), unlike that of other species, which lack an anterior lip. The oval area contains two dark patches (Fig. 77). In posterior view of the epigynum, the lateral plates appear ventrally swollen (Fig. 78). The male differs from others by the shape of the median apophysis in the palpus (Fig. 81).

Paratypes. BRAZIL *Rio de Janeiro:* Itabapoana, ♀ (M. Rosa, MNRJ); Goitacases, Campos, ♀ (M. Rosa, MNRJ). *São Paulo:* Botucatu, Parque Municipal, 5 Nov. 1986, 2♂, 16 Dec. 1986, 2♀ (I. M. P. Rinaldi, L. C. Forte, IMPR, MCZ).

Wagneriana cobella new species
Figures 82–87; Map 3

Holotype. Female holotype from Cuchillo Cebolleta, San Pedro, 1,920 m, Sierra Nevada de Santa Marta, Depto. Magdalena, Colombia, in lower montane forest, 10 May 1975 (J. A. Kochalka), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace yellow-orange. Legs dusky orange, indistinctly ringed. Venter of abdomen black with a pair of light lines. Carapace without macrosetae. Eyes subequal. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with eight tubercles (Fig. 86). Total length 6.2 mm. Carapace 2.8 mm long, 2.0 mm wide. First femur 2.5 mm; patella and tibia 3.1 mm; metatarsus 1.8 mm; tarsus 0.8 mm. Second patella and tibia 2.7 mm; third, 1.6 mm; fourth, 2.5 mm.

Male paratype. Posterior median eyes same diameter as anterior medians, anterior laterals 0.8 diameter of anterior medians, posterior 0.7 diameter. Anterior median eyes slightly more than their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with one short, relatively slender macroseta. Total length 5.5 mm. Carapace 2.7 mm long, 2.2 mm wide. First femur 2.9 mm; patella and tibia 3.1 mm; metatarsus 1.7 mm; tarsus 0.7 mm. Second patella and tibia 2.5 mm; third, 1.5 mm; fourth, 2.1 mm.

Variation. Total length of females 6.2 to 7.4 mm. The specimen from Venezuela has the tip of the epigynum torn off (Fig. 83). The white coloration of the female holotype and of the male paratype was damaged because of the presence of formaldehyde in the alcohol. The Venezuelan paratype has white pigment where the holotype is light on the abdomen.

Diagnosis. The median plate of the epigynum in posterior view is short and wide (Fig. 84) unlike the epigynum of any other species. The male has a characteristically shaped median apophysis distally bent on itself, and a cone-shaped, pointed embolus (Fig. 87).

Natural History. Specimens have been collected at high elevations, 1,560–2,200 m, in cloud forest in Venezuela and in low vegetation in Colombia.

Paratypes. VENEZUELA *Mérida:* La Carboneira, NW Mérida, on road from Mérida to La Azulita, 2,200 m, 11 Jan. 1985, ♀ (J. Palmer, MCZ). COLOMBIA *Magdalena:* San Javier, San Pedro, 1,560 m, 29 Mar. 1975, ♂ (J. Kochalka, MCZ).

Wagneriana lechuza new species
Figures 88–92; Map 3

Holotype. Female holotype from Cueva de La Lechuza, Tingo María, Huánuco, Peru, 31 May 1967 (A. F. Archer, S. Risco), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange to dark brown. Legs orange with irregular black rings. Venter black with an orange longitudinal band on each side. Carapace without macrosetae (Fig. 91). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart.

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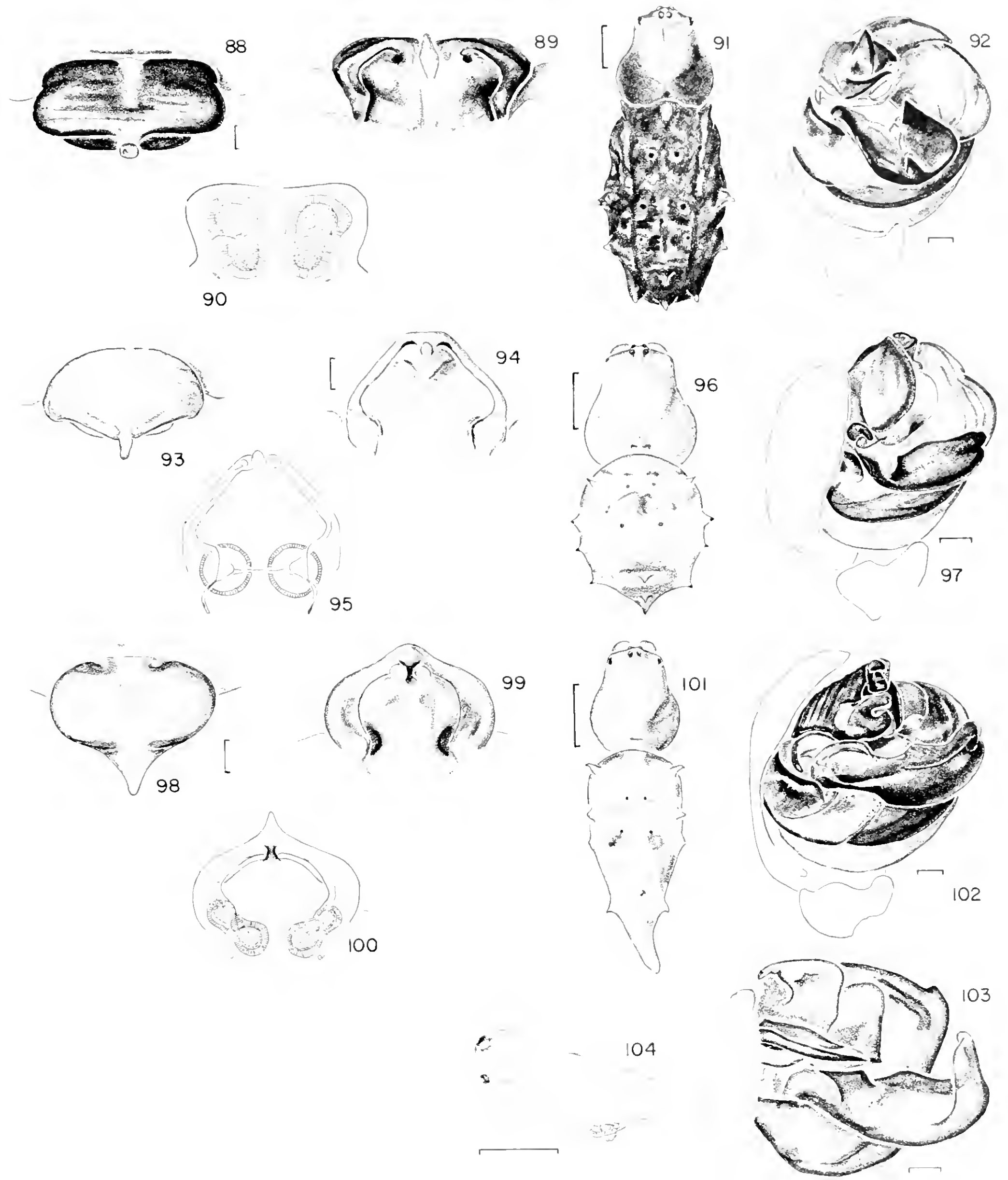
Figures 88–92 *Wagneriana lechuza* n. sp. 88–91. Female. 88. Epigynum, ventral. 89. Epigynum, posterior. 90. Epigynum, cleared. 91 Dorsal 92 Male left palpus.



Figures 93–97. *W. atuna* n. sp. 93–96. Female. 93. Epigynum, ventral. 94. Epigynum, posterior. 95. Epigynum, cleared. 96. Dorsal. 97. Male palpus.

Figures 98–101. *W. juquia* n. sp., female. 98. Epigynum, ventral. 99. Epigynum, posterior. 100. Epigynum, cleared. 101. Dorsal.

Figure 102. *W. carimagua* n. sp., male palpus.

Figures 103–104. *W. uropygialis* (Mello-Leitão)., male. 103. Palpus. 104. Abdomen, lateral.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

Posterior median eyes 0.8 diameter apart. First femur with a distal, mesal field of four macrosetae. Abdomen with four tubercles on each side and two median posteriorly (Fig. 91). Total length 7.2 mm. Carapace 3.1 mm long, 2.5 mm wide. First femur 3.0 mm; patella and tibia 3.5 mm; metatarsus 2.0 mm; tarsus 0.9 mm. Second patella and tibia 3.1 mm; third, 1.9 mm; fourth, 2.9 mm.

Male from Tambopata Reserve. Color as in female. Carapace with many white setae. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.5 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter without macroseta. Fourth femur with seven short macrosetae on tubercles. Abdomen as in female. Total length 7.5 mm. Carapace 3.4 mm long, 2.5 mm wide. First femur 3.4 mm; patella and tibia 4.0 mm; metatarsus 2.2 mm; tarsus 0.9 mm. Second patella and tibia 3.0 mm; third, 2.0 mm; fourth, 2.9 mm.

Illustrations. The illustrations were made from the female holotype and a male from the Tambopata Reserve, Peru.

Note. Male and female were matched by one collection with both sexes.

Variation. Total length of females 6.4 to 9.0 mm, of males 5.9 to 8.5. The largest specimen is the one collected in Espírito Santo, Brazil.

Diagnosis. The epigynum of this species differs by being almost rectangular in ventral view with the posterior margin forming a transverse straight line (Fig. 88) and in posterior view having the median plate constricted in the middle (Fig. 89). The male palpus has a tegulum bearing a projection on the distal edge of the palpus, a squarish median apophysis and a short gently curved embolus (Fig. 92).

Paratypes. PERU *Amazonas:* Alto Río Comaina, Puesto de Vigilancia, 850–1,150 m, 04°27'S, 78°03'W, left bank of Río Marañon 21 Oct.–3 Nov. 1987, 3♀ (D. Silva D., MHNSM). *Huánuco:* Cucharas, Hullaga Valley, Feb.–Apr. 1954, 5♀, ♂ (F. Woytkowski, CAS). *Madre de Dios:* Zona Reservada Tambopata, 23 July 1987, ♀; 30 July 1987, ♂; 23–26 May 1988, ♀; 7 June 1988, 2♀ (D. Silva D., MHNSM); 6 Oct. 1987, ♀ (J. Coddington, D. Silva D., MHNSM); Zona Reservada de Manu, 5 km upstream Pakitza, 11°58'S, 71°18'W, 4 Oct. 1987, ♂ (J. Coddington, D. Silva D., USNM). BRAZIL *Acre:* Rio Purus, NW Sena Madureira Seringal, Santo Antônio, above Manuel Urbano, 15–18 Sept. 1973, ♀ (B. Patterson, MCZ). *Espírito Santo:* Parque Nacional de Sooretama, Linhares, 19°00'S, 40°05'W, 12–27 Oct. 1962, ♀ (P. Pereira, MZSP 7677).

Wagneriana atuna new species
Figures 93–97; Map 3

Holotype. Female holotype from Cali, 1,000 m, Depto. Valle, Colombia, 1 Apr. 1964 (P. B. Schneble), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace dusky orange-yellow. Legs dusky orange with indistinct narrow black rings. Venter of abdomen with a white square between epigynum and spinnerets. Carapace without macrosetae. Eyes small and subequal. Anterior median eyes 2 diameters apart. Posterior median eyes 2.7 diameters apart. Abdomen soft, with 11 tubercles (Fig. 96). Total length 4.5 mm. Carapace 2.1 mm long, 1.9 mm wide. First femur 2.2 mm; patella and tibia 2.5 mm; metatarsus 1.1 mm; tarsus 0.5 mm. Second patella and tibia 2.2 mm; third, 1.2 mm; fourth, 1.8 mm.

Male from Cali. Color as in female but cephalic region light, sides of thoracic region dark. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes 1.3 diameters apart. Fourth trochanter with one short macroseta. Total length 5.2 mm. Carapace 2.1 mm long, 1.6 mm wide. First femur 2.1 mm; patella and tibia 2.3 mm; metatarsus 1.2 mm; tarsus 0.5 mm. Second patella and tibia 1.9 mm; third, 1.2 mm; fourth, 1.7 mm.

Illustrations. The illustrations were made from the female holotype and a male from Cali, Colombia.

Note. The match of males to females is not certain. The male from Cali has relatively larger eyes than the female.

Variation. Total length of females 4.5 to 6.0 mm, of males 4.5 to 5.2. A female from Costa Rica has a long tail and was 9.3 mm total length. The female from Belém, Brazil, has the posterior median plate of the epigynum concave and more sclerotized than that of other specimens.

Diagnosis. In posterior view of the epigynum, the median plate has a transverse groove (Fig. 94). The male has one macroseta on the fourth trochanter and the palpus has the wide cymbium covering most of the radix with the embolus just outside its edge (Fig. 97). The terminal apophysis is rounded on one side and the median apophysis is oval and without large lobes (Fig. 97).

Natural History. The male from Guyana came from a forest savanna.

Distribution. From Costa Rica to Paraguay (Map 3).

Paratypes. COSTA RICA *Heredia:* La Selva, 16 Sept. 1981, ♀ (Coville, MCZ). GUYANA Canje, Ikurua Rivers, Aug.–Dec. 1961, 2♂ (G. Bentley, AMNH); Kartabo, 1920, ♀ (CUC), 1924, ♀ (AMNH). COLOMBIA *Valle:* Atuncela, 800 m, 15 Dec. 1969, ♀ (W. Eberhard 162, MCZ); Cali, 1,000 m, 1976, ♂ (W. Eberhard, MCZ); nr. Cali, 1,000 m, ♀ (W. Eberhard 574, MCZ). PERU *Junín:* Utcuyacu, 1,600–2,200 m, 4 Apr. 1948, ♂ (F. Woytkowski, AMNH). BRAZIL *Pará:* Utinga, Belém, 10–21 Nov. 1963, ♀, doubtful det. (Oliveira, P. Wygodzinsky, AMNH). *Rio de Janeiro:* Rio de Janeiro, ♀ (MNRJ). *Mato Grosso:* 260 km N Xavantina, 12°49′S, 51°46′W, Feb.–Apr. 1969, ♂ (Xavantino-Cochimbo Exped., MCZ). *Rio Grande do Sul:* Parque Zool. Gico, Sapucaia do Sul, 20 Jan. 1986, ♀ (A. Tavares, MCN 14339). PARAGUAY *Amambay:* Parque Nacional Cerro Corá, 28 May–9 June 1982, ♀ (J. A. Kochalka, IBNP).

Wagneriana juquia new species
Figures 98–101; Map 3

Holotype. Female holotype from Fazenda Poço Grande, Juquiá, São Paulo State, Brazil, 21–26 July 1949 (F. Lane), in MZSP no. 7360. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, sides of thoracic region darker. Legs light orange. Venter of abdomen between epigynum and spinnerets underlain by white pigment, dusky behind epigynum. Carapace without macrosetae. Posterior median eyes 1.2 diameters of anterior medians, anterior laterals 0.8 diameter, posterior laterals 1 diameter. Anterior median eyes 1.4 diameters apart. Posterior median eyes 1.2 diameters apart. Abdomen with 11 tubercles (Fig. 101). Total length 5.5 mm. Carapace 2.0 mm long, 1.5 mm wide. First femur 2.0 mm; patella and tibia 2.3 mm; metatarsus 1.2 mm; tarsus 0.5 mm. Second patella and tibia 1.9 mm; third, 1.0 mm; fourth, 1.7 mm.

Illustration. The female holotype was illustrated.

Note. Wagneriana juquia may belong with the male of *W. uropygialis.*

Variation. Total length of females 5.0 to 7.0 mm. The holotype is the only specimen with a long tail (Fig. 101).

Diagnosis. Unlike other species *W. juquia* has a dark, sclerotized septum ventrally on the posterior face, below the tip of the epigynum (top of Fig. 99).

Paratypes. BRAZIL *São Paulo:* Fazenda Poço Grande, Juquiá, 21–26 July 1949, 3♀ (F. Lane, MZSP 7326,7330); Barueri, 16 Jan. 1966, ♀ (K. Lenko, MZSP 5582); São José Barreiro, S Bocaina, 1,960 m, Nov. 1968, ♀ (M. Alvarenga, AMNH). PARAGUAY *Concepción:* Territ. Fonciere, 1908, ♀ (E. Reimoser, NHMW). ARGENTINA *Río Negro:* El Bolsón area, 1965–1966, ♀ (A. Kovacs, AMNH).

Wagneriana carimagua new species
Figure 102; Map 3

Holotype. Male holotype from Carimagua, 100 m, Dpto. Meta, Colombia, Oct. 1973, grass and brush

along fence (W. Eberhard), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace light orange, sides of thoracic region dusky anteriorly. Sternum dusky with three pairs of clear spots. Coxae yellowish; legs yellowish with dusky spots and rings. Abdomen dusky. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 1.5 diameters apart. Posterior median eyes slightly less than their diameter apart. Fourth trochanter with two short macrosetae. Abdomen with a pair of anterior tubercles, and posteriorly two median tubercles in a line. Total length 5.8 mm. Carapace 2.9 mm long, 2.3 mm wide. First femur 3.2 mm; patella and tibia 3.8 mm; metatarsus 2.3 mm; tarsus 1.0 mm. Second patella and tibia 3.0 mm; third, 1.8 mm; fourth, 2.9 mm.

Note. This might be the male of *W. jacaza.*

Diagnosis. The two elongate lobes of the median apophysis (Fig. 102) differ from that of all other species.

Wagneriana uropygialis (Mello-Leitão), new combination
Figures 103, 104; Map 3

Paraverrucosa uropygialis Mello-Leitão, 1944: 334. Male holotype from Tigre, Buenos Aires Prov., Argentina, in MLP, examined. Brignoli, 1983: 278.

Description. Male holotype. Carapace, sternum, legs yellow-white. Dorsum of abdomen blackish with median dorsal area lighter, a pair of white spots on anterior margin separated by black (Fig. 104); venter black with some white pigment spots near spinnerets (Fig. 104). Eyes subequal. Anterior median eyes 1.2 diameters apart. Posterior median eyes slightly more than a diameter apart. Abdomen elongate (shrivelled) with a posterior line of three tubercles (Fig. 104). Total length 4.2 mm. Carapace 2.1 mm long, 1.4 mm wide. First femur 1.7 mm; patella and tibia 2.2 mm; metatarsus 1.1 mm; tarsus 0.7 mm. Second patella and tibia 1.7 mm; third, 1.2 mm; fourth, 1.7 mm.

Note. The shape of the paramedian apophysis, an L on its side (Fig. 103), suggests that this species is a *Wagneriana*. The female *W. juguia* may be conspecific.

Diagnosis. This male differs from others by the relatively long median apophysis (Fig. 103).

Wagneriana heteracantha (Mello-Leitão), new combination
Figures 105–109; Map 4

Actinosoma heteracantha Mello-Leitão, 1943: 174, fig. 15, ♀. Female holotype from Rio Grande do Sul, Brazil, in MNRJ, lost. Brignoli, 1983: 255.

[?] *Marxia labidura* Mello-Leitão, 1943: 184, fig. 22, ♂. Male holotype from Rio Grande do Sul, in MNRJ, lost. DOUBTFUL NEW SYNONYMY.

Note. The type of *Marxia labidura* is lost. Its size suggests that it may have been this species or perhaps W. palaestris.

Description. Female from Canela, Rio Grande do Sul. Cephalic region orange with a dark transverse band behind eyes and two dark patches, sides of thoracic region brown-black. Legs yellowish with brown to black rings. Venter of abdomen with a black square having a white line on each side enclosing three pairs of white spots. Carapace without macrosetae. Pos-

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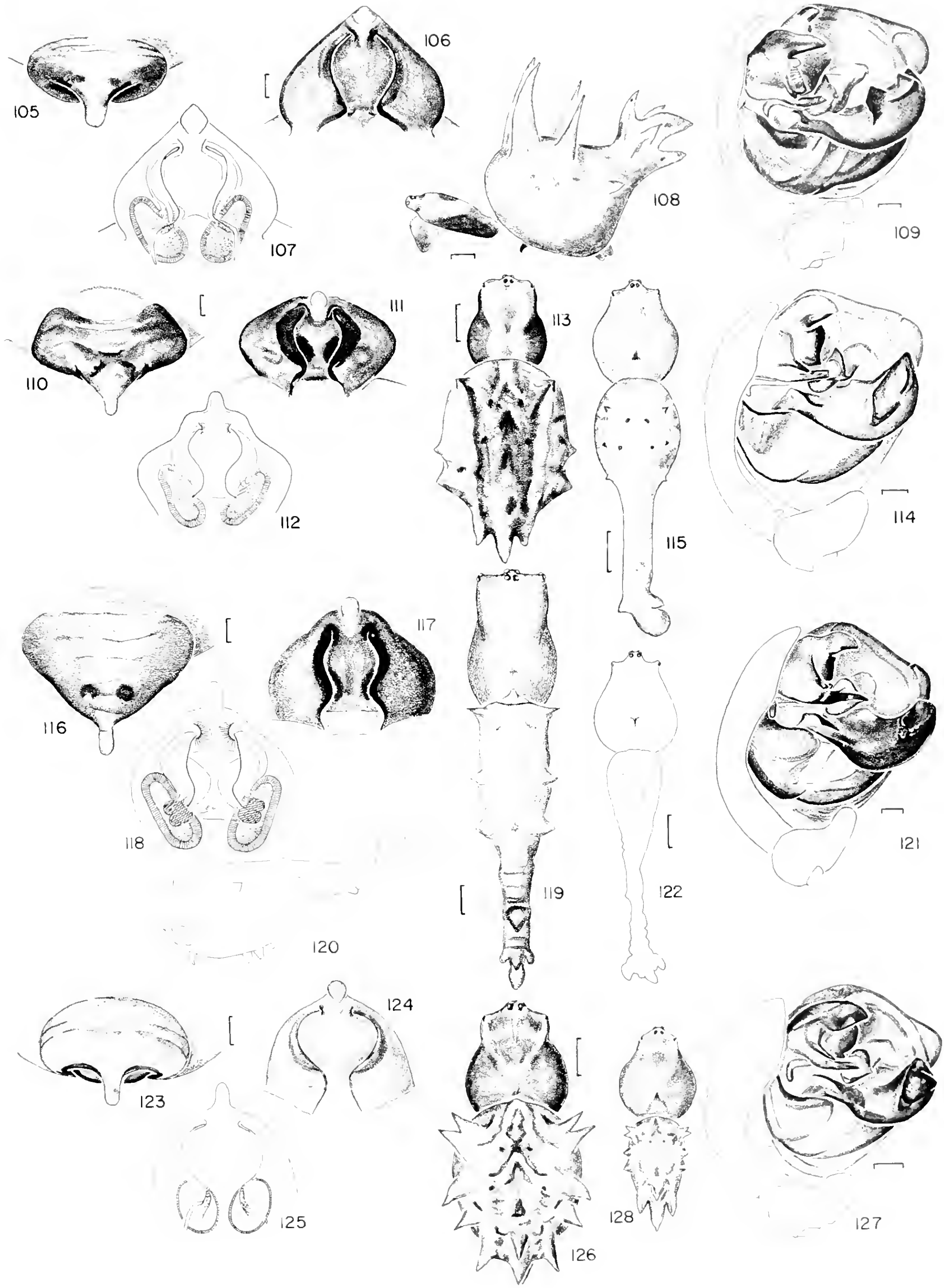
Figures 105–109. *Wagneriana heteracantha* (Mello-Leitão). 105–108. Female. 105. Epigynum, ventral. 106. Epigynum, posterior. 107. Epigynum, cleared. 108. Lateral. 109. Male left palpus.

Figures 110–115. *W. eupalaestris* (Mello-Leitão). 110–113. Female. 110. Epigynum, ventral. 111. Epigynum, posterior. 112. Epigynum, cleared. 113. Dorsal. 114, 115. Male. 114. Palpus. 115. Dorsal.

Figures 116–122. *W. neglecta* (Mello-Leitão). 116–120. Female. 116. Epigynum, ventral. 117. Epigynum, posterior. 118. Epigynum, cleared. 119. Dorsal. 120. Abdomen, lateral. 121, 122. Male. 121. Palpus. 122. Dorsal.

Figures 123–128. *W. uzaga* n. sp. 123–126. Female. 123. Epigynum, ventral. 124. Epigynum, posterior. 125. Epigynum, cleared. 126. Dorsal. 127, 128. Male. 127. Palpus. 128. Dorsal.

Scale lines 1.0 mm, genitalia 0.1 mm.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terior median eyes 1.2 diameters of anterior medians, anterior laterals 1.1 diameters, posterior laterals 1 diameter. Anterior median eyes 1.1 diameters apart. Posterior median eyes 1.5 diameters apart. Abdomen with 11 drawn out tubercles (Fig. 108). Total length 12.0 mm. Carapace 4.1 mm long; 3.1 mm wide. First femur 3.8 mm; patella and tibia 4.4 mm; metatarsus 2.3 mm; tarsus 1.1 mm. Second patella and tibia 3.8 mm; third, 2.3 mm; fourth, 3.4 mm.

Male from Carmo do Rio Claro, Minas Gerais. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes slightly more than their diameter apart. Fourth trochanter with two short macrosetae. Abdomen with a tail. Total length 9.0 mm. Carapace 3.4 mm long, 2.5 mm wide. First femur 3.2 mm; patella and tibia 3.5 mm; metatarsus 2.1 mm; tarsus 0.9 mm. Second patella and tibia 2.9 mm; third, 1.8 mm; fourth, 2.7 mm.

Illustrations. The female from Canela and the male from Carmo do Rio Claro were illustrated.

Note. Males and females have been collected together.

Variation. Total length of females 11 to 13.7 mm, of males 5.6 to 9.7. Males have one tubercle on the fourth trochanter; some males have one tubercle on one side, two on the other.

Diagnosis. The female can be separated from others by the long abdominal tubercles (Fig. 108), and the shape of the epigynum. The posterior median plate of the epigynum is as wide as the lateral plates in posterior view (Fig. 106), while in both *W. neglecta* (Fig. 117) and *W. eupalaestris* (Fig. 111) the median plate is narrower. The male palpus has a distal lobe on the tegulum (top of Fig. 109) and the median apophysis has a median vertically placed keel, neither structure being present in the two related species.

Distribution. From Minas Gerais State of Brazil to Río Negro Prov. of Argentina (Map 4).

Records. BRAZIL *Minas Gerais:* ♀, ♂ (NHMW); Carmo do Rio Claro, ♀, ♂ (J. C. Carvalho, MNRJ). *São Paulo:* São José Barreiro, S Bocaina, 1,960 m, Nov. 1968, ♂ (A. Alvarenga, MCZ). *Paraná:* Río Negro, 2♂ (MNRJ); Curitiba, 10 Nov. 1938, 2♀ (F. S. Pereira, MZSP 3088, 132); Cavinna[?] 1947, ♀ (A. Maller, AMNH). *Santa Catarina:* Pinhal, Dec. 1947, ♂ (A. Maller, AMNH). *Rio Grande do Sul:* Taquara, 18 Jan. 1983, ♀ (T. Lema, MCN 11444); Canela, 7 Oct. 1967,♀ (R. Teixeira, MCN 0643). ARGENTINA *Misiones:* Parque Nacional Iguazu, Oct. 1977, ♀ (M. E. Galiano, MEG); Eldorado, 1 Sept.–15 Nov., ♂ (A. Kovacs, AMNH). *Río Negro:* El Bolsón area, 1965–1966, ♀, 2♂ (A. Kovacs, AMNH).

Wagneriana eupalaestris (Mello-Leitão), new combination
Figures 110–115; Map 4

Edricus eupalaestris Mello-Leitão, 1943: 177, fig. 17, ♂. Male holotype from Rio Grande do Sul, Brazil, in MNRJ, examined.

Paraverrucosa eupalaestrus:—Mello-Leitão, 1947a: 13. Brignoli, 1983: 278.

Description. Female from Campos de Jordão, São Paulo. Carapace orange, darker in midline, sides of thoracic region black. Sternum black. Coxae yellowish; legs yellowish with indistinct dark rings. Venter of abdomen with a black longitudinal band. Carapace without macrosetae. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter of anterior medians. Anterior median eyes 1.5 diameters apart. Posterior median eyes 1.5 diameters apart. Lateral eyes separated by almost their diameter. Abdomen with 10 tubercles, the one above spinnerets missing (Fig. 113). Total length 7.3 mm. Carapace 2.9 mm long, 2.1 mm wide. First femur 2.5 mm; patella and tibia 2.9 mm; metatarsus 1.5 mm; tarsus 0.8 mm. Second patella and tibia 2.4 mm; third, 1.5 mm; fourth, 2.3 mm.

Male holotype. Color as in female. Pos-

terior median eyes same diameter as anterior medians, lateral eyes 0.9 diameter of anterior medians. Anterior median eyes 1.1 diameters apart. Posterior median eyes 1.1 diameters apart. Fourth trochanter with one short macroseta on one side, two on other. Abdomen with tail (Fig. 115). Total length 7.5 mm. Carapace 2.7 mm long, 2.1 mm wide. First femur 3.0 mm; patella and tibia 3.5 mm; metatarsus 2.0 mm; tarsus 0.8 mm. Second patella and tibia 2.7 mm; third, 1.7 mm; fourth, 2.4 mm.

Illustrations. The female from Campos do Jordão, São Paulo State, the male from Viamão, Rio Grande do Sul State, were illustrated.

Variation. Total length of females 7.3 to 11.2 mm, of males 5.3 to 9.2. A large male from Viamão is most like the holotype of *W. eupalaestris*, including the long abdomen. In some females the abdomen has a tail.

Diagnosis. This species is smaller than *W. neglecta*; there does not seem to be a size overlap. The female usually has a short abdomen and relatively short abdominal tubercles (Fig. 113). The female differs from that of *W. heteracantha* in having the median plate of the epigynum narrower in posterior view than the lateral plates (Fig. 111). The male differs from *W. neglecta* by having one or two macrosetae on the fourth coxa, from *W. heteracantha* by lacking the lobe at the distal edge of the tegulum and the median keel of the median apophysis (Fig. 114).

Distribution. From Minas Gerais State of Brazil to Misiones Prov. of Argentina (Map 4).

Records. BRAZIL *Minas Gerais:* 2♀ (NHMW). *São Paulo:* Boracéia, Salesópolis, 21–25 Oct. 1963 (Oliveira, P. Wygodzinsky, AMNH); Campos do Jordão, Mar. 1945, ♀ (P. Wygodzinsky, MZSP 4631); Dec. 1944, ♀ (F. Lane, MZSP 4645); 3 Jan. 1948, 3♀ (F. Lane, MZSP 7323); Cantareira, Capital, Nov. 1951, ♀ (Carrera, Andreotta, MZSP 8281). *Rio Grande do Sul:* São Francisco de Paula, ♀ (P. P. Buck, MNRJ); Morro de Côco, Viamão, 25 July 1985, ♂ (A. A. Lise, MCN 13359). ARGENTINA *Misiones:* Eldorado, 1 Sept.–15 Nov. 1964, ♀ (A. Kovacs, AMNH).

Wagneriana neglecta (Mello-Leitão), new combination
Figures 116–122; Map 4

Paraverrucosa neglecta Mello-Leitão, 1939a: 65, figs. 38–40, ♂. Male holotype from Paraguay, in NMB, examined. Roewer, 1942: 870. Bonnet, 1958: 3339.

Verrucosa longicauda Mello-Leitão, 1947b: 251. Immature male and immature female syntypes from Barigui, Municip. Curitiba, Paraná State, Brasil, in MHNC, examined. Brignoli, 1983: 280. NEW SYNONYMY.

Wagneriana tuberculicauda di Caporiacco, 1947: 25; 1948: 657, figs. 64, 65, ♀. Female holotype from near Demerera River, Guyana, in MZUF, examined. Brignoli, 1983: 281. NEW SYNONYMY.

Description. Female from Kartabo, Guyana. Carapace orange-brown darkest on sides of thoracic region; light between median eyes. Legs orange to brown, femora darkest. Venter black. Carapace without macrosetae. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 1.4 diameters apart. Abdomen with three pairs of lateral tubercles and 3 to 5 pairs of posterior ones (Fig. 119). Total length 15 mm. Carapace 5.4 mm long, 3.5 mm wide. First femur 4.1 mm; patella and tibia 5.3 mm; metatarsus 2.7 mm; tarsus 1.1 mm. Second patella and tibia 4.7 mm; third, 2.7mm; fourth, 3.8 mm.

Male from Trinidad. Color as in female except for carapace brown, lighter in midline, and light between eyes. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.5 diameter, posterior laterals 0.4. Anterior median eyes 0.7 diameter apart. Posterior median eyes 1.3 diameters apart. Fourth trochanter without macroseta. Abdomen with tubercles at posterior end (Fig. 122). Total length 11.4 mm. Carapace 3.9 mm long, 2.8 mm wide. First femur 3.9 mm; patella and tibia 4.4 mm; metatarsus 2.0 mm; tarsus 0.7 mm.

Second patella and tibia 3.4 mm; third, 2.0 mm; fourth, 2.7 mm.

Illustrations. Illustrations of the female were made from the holotype of *W. tuberculicauda*, those of the male from a specimen from Trinidad.

Variation. Total length of females 12.3 to 16 mm, of males 9.5 to 10.7.

Diagnosis. *Wagneriana neglecta* is larger than *W. eupalaestris* and *W. heteracantha* and both sexes have a long tail (Figs. 119, 122); in the two related species only the male may have a long tail. As in the related two species, *W. neglecta* lacks a ventral tubercle at the tip of the tail. The posterior median plate of the epigynum is relatively narrow as in *W. eupalaestris* (Fig. 117). The male lacks macrosetae on the trochanter unlike *W. eupalaestris* and *W. heteracantha.* The truncate distal end of the median apophysis (Fig. 121) is smaller than that of *W. eupalaestris* (Fig. 114) and *W. uzaga* (Fig. 127).

Natural History. Males were collected by sweeping brush in Trinidad.

Distribution. Trinidad to Jujuy Prov. of Argentina (Map 4).

Records. LESSER ANTILLES *Trinidad:* Simla, 6.4 km N Arima, 10 May 1981, 2♂ (R. West, MCZ). GUYANA *Bartica Distr.:* Kartabo, 1924, ♀ (W. Beebe, AMNH). BRAZIL *Goias:* Fazenda Aceiro, Jataí, Oct. 1962, ♀ (MZSP 7863). *Paraná:* Rolândia, 1948, ♀, 2♂ (A. Maller, AMNH). *Rio Grande do Sul:* Garruchos, São Borja, 7 Dec. 1985, ♀ (A. A. Lise, MCN 3203); São Gabriel, Jan. 1924, ♀ (A. Roman, NRMS). PARAGUAY *Chaco:* Parque Nacional Defensores del Chaco, Cerro León, 19–27 Nov. 1984, ♀ (J. A. Kochalka, IBNP). BOLIVIA *Santa Cruz:* Buena Vista, Feb. 1951, ♂ (R. F. Prosea, MLP). ARGENTINA *Jujuy:* Yuto, El Pantanoso, Mar. 1967, ♀ (M. E. Galiano, MEG).

Wagneriana uzaga new species

Figures 123–128; Map 4

Holotype. Female holotype from Parque Nacional Iguazu, Misiones Prov., Argentina, Jan. 1966 (M. E. Galiano), in MACN no. 8791. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace yellowish, cephalic region with two pairs of darker patches, sides of thoracic region dark dusky. Legs yellowish with dusky rings. Venter of abdomen black with a white line on each side. Carapace without macrosetae. Eyes small and subequal. Anterior median eyes 2.2 diameters apart. Posterior median eyes 2.5 diameters apart. Lateral eyes separated by their diameter. Abdomen with anterior lateral double tubercles (Fig. 126). Total length 6.5 mm. Carapace 3.2 mm long, 2.4 mm wide. First femur 2.5 mm; patella and tibia 2.9 mm; metatarsus 1.5 mm; tarsus 0.7 mm. Second patella and tibia 2.6 mm; third, 1.6 mm; fourth, 2.4 mm.

Male from Dpto. Chaco, Paraguay. Much darker than female with a light, longitudinal band on each side of abdomen. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.5 diameters apart. Fourth trochanter with two short macrosetae, a thick one on a tubercle and a thin one not on a tubercle. Abdomen with anterior pair of double tubercles (Fig. 128). Total length 5.0 mm. Carapace 2.5 mm long, 1.8 mm wide. First femur 2.3 mm; patella and tibia 2.7 mm; metatarsus 1.3 mm; tarsus 0.7 mm. Second patella and tibia 2.2 mm; third, 1.1 mm; fourth, 1.7 mm.

Illustrations. Figures 123–125 were made from the holotype, Figure 126 from a female from Paraguay, the figures of the male from a specimen from Chaco, Paraguay.

Note. Female and males were matched because both have the anterior tubercle on the abdomen double and because of the similarity of their genitalia to those of *W. eupalaestris* and *W. heteracantha.*

Variation. Total length of females 6.0 to 7.1 mm, of males 5.0 to 5.7.

Diagnosis. This species differs from most similar species by having the anterior lateral tubercle of the abdomen double (Figs. 126, 128). It is most similar to *W. spicata*

found in Mexico but differs by being smaller and having weakly sclerotized, pear-shaped seminal receptacles (Fig. 125). The posterior view of the epigynum differs from that of *W. eupalaestris* (Fig. 111) by having a wider median plate (Fig. 124). The male differs from *W. eupalaestris* in the sculpturing of the blunt end of the median apophysis (Fig. 127).

Distribution. Mato Grosso do Sul State of Brazil to Paraguay and Misiones Prov. of Argentina (Map 4).

Paratypes. BRAZIL *Mato Grosso do Sul:* Três Lagoas, 21 Sept. 1964, ♂ (MZSP 3631). *Paraná:* Rolândia, 1948, ♀ (A. Maller, AMNH). PARAGUAY *Concepción:* nr. Concepción, 1956, ♂ (C. J. D. Brown, MCZ). *Chaco:* Parque Nacional Defensores del Chaco, Misión Cué, 24 Aug. 1983, ♂ (J. A. Kochalka, IBNP). *Central:* San Lorenzo, 8 Aug. 1986, ♀ (J. A. Kochalka, IBNP). ARGENTINA Pto. Aguirre [?], 27 Dec. 1933, ♀ (Hayward, MACN).

Wagneriana spicata (O. P.-Cambridge) Figures 129–133; Map 4

Epeira spicata O. P.-Cambridge, 1889: 45, pl. 6, fig. 4, imm. Immature male holotype from Valley of the Motagua, Guatemala, in BMNH, examined.

Turckheimia armata O. P.-Cambridge, 1893: 114, pl. 14, fig. 11, ♀. Female holotype from Rincón, Guerrero [16 km S Chilpancingo], Mexico, 2,800 ft [850 m], in BMNH, examined. First synonymized by F. P.-Cambridge, 1904.

Wagneriana spicata:—F. P.-Cambridge, 1904: 499, pl. 47, figs. 19, 20, ♀, ♂. Roewer, 1942: 880. Bonnet, 1959: 4803.

Description. Female from Chiapas. Carapace orange to black-brown. Legs orange with black rings and black spots. Venter of abdomen black with paired and unpaired light spots. Carapace with two macrosetae (Fig. 132). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.7 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes their diameter apart. Abdomen with 13 tubercles, the anterior pair double (Fig. 132). Total length 11.4 mm. Carapace 4.6 mm long, 3.6 mm wide. First femur 4.2 mm; patella and tibia 5.4 mm; metatarsus 2.8 mm; tarsus 1.1 mm. Second patella and tibia 4.5 mm; third, 2.7 mm; fourth, 4.3 mm.

Male from Chiapas. Color as in female but darker. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two short macrosetae. Abdomen as in female. Total length 8.7 mm. Carapace 4.5 mm long, 3.6 mm wide. First femur 4.6 mm; patella and tibia 5.7 mm; metatarsus 3.1 mm; tarsus 1.2 mm. Second patella and tibia 4.4 mm; third, 2.7 mm; fourth, 4.2 mm.

Natural History. Immature specimens 2.7 mm long have the macrosetae on the carapace and the bifid spine on the abdomen.

Variation. Total length of females 8.2 to 12.3 mm, of males 7.6 to 8.3. The illustrations were made from specimens from Chiapas, Mexico.

Diagnosis. The pair of double anterior tubercles (Fig. 132) separates females from other species in Mexico and Central America. In posterior view of the epigynum the narrow median plate is distinctive (Fig. 130). Males can be separated from most other species by having two macrosetae on the fourth trochanter, by the two lobes of the tegulum, one apical and one lateral, and by the shapes of median and terminal apophyses (Fig. 133).

Distribution. Mexico to Costa Rica (Map 4).

Records. MEXICO *Sonora:* Minas Nuevas, 8 Aug. 1952, ♀ (P., C. Vaurie, AMNH). *Nayarit:* 3.2 km N Sayulita, 19 Nov. 1976, ♀ (D. D. Wilder, CAS); 12 km E San Blas, 17 Oct. 1973, ♀ (S. C. Williams *et al.*, CAS); 24 to 32 km W Tepic, Sept. 1961, ♂ (A. Aschwanden, AMNH). *Jalisco:* Esta. Biol. Chamela, Sept. 1988, 4♀, 2♂, 10 imm. (W. Eberhard, MCZ); Puerto Vallarta, Aug., Sept. 1957, 2♂ (J. Comstock, AMNH). *Colima:* Armeria, 1 Aug. 1954, ♂ (W. J. Gertsch, AMNH); Velle Verde, 1 Aug. 1954, ♂ (W. J. Gertsch, AMNH). *Veracruz:*

Puente National, 3 Aug. 1956, ♀ (R. Dreisbach, MCZ). *Oaxaca:* 3 km SE Niltepec, 16 Aug. 1966, ♂ (J., W. Ivie, AMNH); San Gerónimo, 1909, ♀ (A. Petrunkevitch, AMNH). *Chiapas:* nr. Huehuetan, 31 July 1950, ♀, ♂ (C., M. Goodnight, AMNH); Puerto Madero, Puerto de San Benito, 2 Aug. 1950, 3♀, ♂, 2 imm. (C., M. Goodnight, AMNH); Tonala, 1909, ♀ (A. Petrunkevitch, AMNH). COSTA RICA *San José:* Santa María Dota, 09°39′N, 83°57′W, 2♀ (Tristan, MCZ). *Guanacaste:* Finca Palo Verde, 14 July 1979, ♀ (J. Coddington, MCZ).

Wagneriana gavensis (Camargo), new combination

Figures 134–139; Map 4

Wixia gavensis Camargo, 1950: 231, pl. 1, figs. 1, 2, 5, pl. 2, fig. 6, pl. 3, fig. 1, pl. 4, figs. 1–3, 5, ♂. Male holotype from Gávea, Rio de Janeiro State, Brazil, in MZSP no. C1348. Brignoli, 1983: 281.

Description. Female from Angra dos Reis. Carapace orange-brown, lighter around eyes and a pair of large light patches on thoracic region. Legs yellowish with wide brown rings. Venter of abdomen dark dusky. Carapace without macrosetae. Posterior median eyes large, 1.4 diameters of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Abdomen with 9 tubercles, the anterior laterals double (Fig. 138). Total length 6.5 mm. Carapace 3.2 mm long, 2.5 mm wide. First femur 2.5 mm; patella and tibia 3.1 mm; metatarsus 1.8 mm; tarsus 0.8 mm. Second patella and tibia 2.8 mm; third, 1.8 mm; fourth, 2.7 mm.

Male from Represa. Color dark brown to black. Posterior median eyes 1.5 diameters of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.7 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes slightly more than their diameter apart. Fourth trochanter without macroseta. Total length 5.0 mm. Carapace 3.0 mm long, 2.3 mm wide. First femur 2.5 mm; patella and tibia 2.9 mm; metatarsus 1.7 mm; tarsus 0.7 mm. Second patella and tibia 2.5 mm; third, 1.6 mm; fourth, 2.3 mm.

Illustrations. Figures 134, 136–138 were made from a female from Angra dos Reis, Figure 135 from a female from Teresópolis, Figure 139 from a male from Paineiras, Rio de Janeiro.

Note. Both males from Rio de Janeiro State are in poor condition, they may once have been dry. The males were not collected with a female but were matched because of the similar large median eyes and because both female and male genitalia are similar to those of *W. iguape*. In a male from São Paulo State, the shape of the palpal sclerites, the median apophysis, tegulum, and conductor is intermediate beween *W. gavensis* and *W. iguape*, but the embolus is sickle-shaped as in *W. gavensis*.

Diagnosis. The female is separated from others by the long, wide epigynum having transverse grooves on the venter surrounded by a lip (Figs. 134, 135), the male by the elongate, projecting median apophysis and sickle-shaped embolus (Fig. 139).

Distribution. Rio de Janeiro and São Paulo States of Brazil (Map 4).

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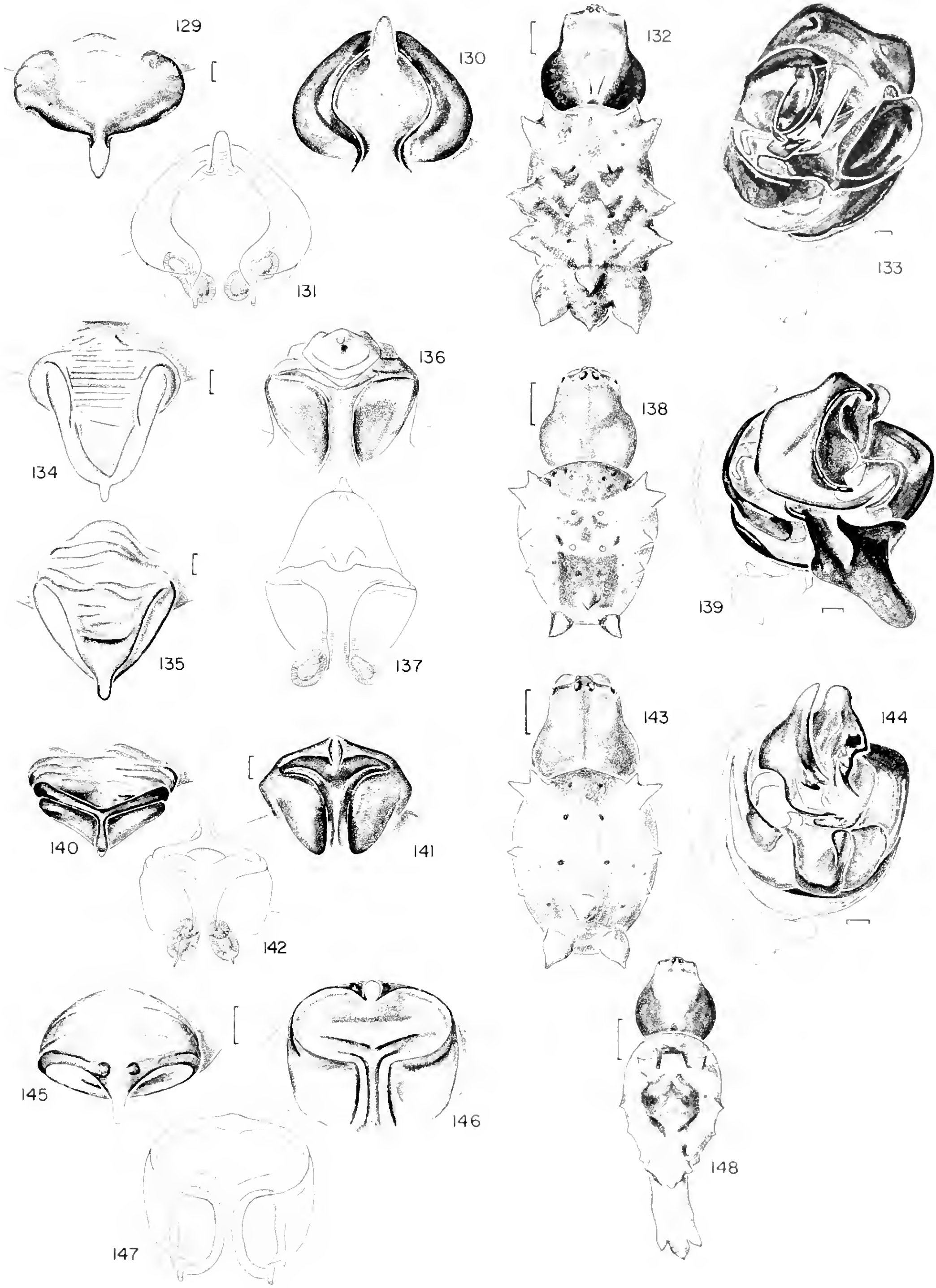
Figures 129–133. *Wagneriana spicata* (O. P.-Cambridge). 129–132. Female. 129. Epigynum, ventral. 130. Epigynum, posterior. 131. Epigynum, cleared. 132. Dorsal. 133. Left male palpus.

Figures 134–139. *W. gavensis* (Camargo). 134–138. Female. 134, 135. Epigynum, ventral. 136. Epigynum, posterior. 137. Epigynum, cleared. 138. Dorsal. 139. Male palpus.

Figures 140–144. *W. iguape* n. sp. 140–143. Female. 140. Epigynum, ventral. 141. Epigynum, posterior. 142. Epigynum, cleared. 143. Dorsal. 144. Male palpus.

Figures 145–148. *W. madrejon* n. sp., female. 145. Epigynum, dorsal. 146. Epigynum, posterior. 147. Epigynum, cleared. 148. Dorsal.

Scale lines. 1.0 mm, genitalia, 0.1 mm.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Paratypes. BRAZIL *Rio de Janeiro:* Angra dos Reis, 23 Mar. 1951, ♀ (W. Bokermann, MZSP 7702); Teresópolis, 900–1,200 m, 7–9 Nov. 1945, ♀, Mar. 1946, ♀ (H. Sick, AMNH); Paineiras, Rio de Janeiro, Aug. 1961, ♂ (M. Alvarenga, AMNH); Reprêsa, Rio Grande, Feb. 1976, ♂ (M. Alvarenga, AMNH). *São Paulo:* São José do Barreiro, S Bocaina, 1,960 m, Nov. 1968, ♂ (M. Alvarenga, AMNH).

Wagneriana iguape new species
Figures 140–144; Map 4

Holotype. Female holotype from Iguape, São Paulo State, Brazil (Leonardos), in MNRJ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange-brown. Legs dusky orange with indistinct dark rings. Venter brown between epigynum and spinnerets, a lighter band on each side. Carapace without macrosetae. Cephalic region bulging, eyes large, posterior median eyes with large black rings. Posterior median eyes 1.5 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes 0.5 diameter apart. Posterior median eyes 0.7 diameter apart. Abdomen with three pairs of lateral tubercles, the first double, one pair posterior, and only one median posterior (Fig. 143). Total length 7.5 mm. Carapace 3.2 mm long, 2.4 mm wide. First femur 2.8 mm; patella and tibia 3.4 mm; metatarsus 1.8 mm; tarsus 0.8 mm. Second patella and tibia 2.9 mm; third, 1.9 mm; fourth, 2.7 mm.

Male from São Paulo State. Color as in female but carapace with a median brown streak and brown bands on sides of thoracic region. Thoracic depression a cross shape. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter without macroseta. Abdomen with three pairs of tubercles, the most anterior pair double, and a small posterior median tubercle. Total length 5.5 mm. Carapace 2.8 mm long, 2.3 mm wide. First femur 2.5 mm; patella and tibia 3.1 mm; metatarsus 1.7 mm; tarsus 0.9 mm. Second patella and tibia 2.5 mm; third, 1.5 mm; fourth, 2.3 mm.

Illustrations. The illustrations were made from the holotype and a male from São Paulo State.

Note. Male and female have been matched because both have the double anterior tubercle on the abdomen.

Variation. Total length of females 5.5 to 7.7 mm, of males 5.1 to 5.5.

Diagnosis. This species is separated from others by the large posterior median eyes and the double tubercle on the anterior of the abdomen (Fig. 143). Both characters are present in females and males. In ventral view the epigynum has a raised T-shaped bar (Fig. 141). The palpus has a large conductor with a distal spherical knob (Fig. 144).

Distribution. Rio de Janeiro State of Brazil to Paraguay (Map 4).

Paratypes. BRAZIL *Rio de Janeiro:* Itatiaia, Dec. 1966, imm. (H. Reichardt, MZSP 7231). *São Paulo:* Guaianases, Feb. 1950, ♀ (M. Carrero, MZSP 7231); Rincão, Nov. 1947, ♀ (Goff, MZSP 7781); Ilha São Sebastião, 23 Mar. 1951, ♀ (H. Urban, MZSP 7215); Cocais, Apr. 1950, ♂ (H. Urban MZSP 7359); Ribeirão Pires, Cidade São Paulo, 700–800 m, Dec. 1945, ♂ (H. Sick AMNH). *Paraná:* Cataratas do Iguaçu, 24 Mar. 1985, ♂ (H., L. Levi, MCZ). *Santa Catarina:* Pinhal, Apr., May 1947, 6♀ (A. Maller, AMNH). *Rio Grande do Sul:* Itaimbezinho, Cambará do Sul, 27 Apr. 1985, ♀, 18 May 1985, ♀ (A. A. Lise, MCN 13289, 13310); São Francisco de Paula, 4 May 1974, ♀, 5 Jan. 1985, ♂ (A. A. Lise, MCN 2165, 12728); Triunfo, 21 Sept. 1989, ♂ (E. H. Buckup, MCN 18652). PARAGUAY *Alto Paraná:* Italo Reserve, 19 June 1984, ♂ (L. Baert, J. P. Malfait, IRSNB).

Wagneriana madrejon new species
Figures 145–148; Map 4

Holotype. Female holotype from Madrejón, Parque Nacional Defensores del Chaco, Depto. Chaco, Paraguay, 12 Dec. 1981 (J. A. Kochalka), in IBNP. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Cephalic region orange with some white setae. Sides of thoracic region brown to black. Legs yellowish with black rings. Venter of abdomen with white pigment between epigynum and spinnerets. Carapace without macrosetae. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 17 tubercles, 4 pairs on sides, 3 proximal and 3 distal on tail and 3 ventrally on tail (Fig. 148). Total length 8.3 mm. Carapace 2.3 mm long, 2.0 mm wide. First femur 2.5 mm; patella and tibia 2.9 mm; metatarsus 1.4 mm; tarsus 0.6 mm. Second patella and tibia 2.4 mm; third, 1.5 mm; fourth, 2.2 mm.

Diagnosis. The abdomen has 17 tubercles, more than any other species (Fig. 148). In posterior view, unlike that of other species, the epigynum has a T-shaped, raised fold, with the vertical member of the T between the lateral plates (Fig. 146).

Wagneriana huanca new species
Figures 149–153; Map 4

Holotype. Female holotype from Huancabamba, Quebrada Castillo, NW of Iscozacin, 345 m, Pasco, Peru, 10°10'S, 75°15'W, 13 Sept. 1987 (D. Silva D.), in MHNSM. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange-brown to brown with white setae. Legs yellow, ringed dark brown. Venter of abdomen with white pigment in center. Carapace with two macrosetae. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Abdomen [damaged], with three pairs of lateral and three posterior median tubercles (Fig. 153). Total length 11.0 mm. Carapace 4.2 mm long, 3.2 mm wide. First femur 4.7 mm; patella and tibia 5.5 mm; metatarsus 2.9 mm; tarsus 1.0 mm. Second patella and tibia 4.8 mm; third, 2.6 mm; fourth, 3.9 mm.

Illustrations. Figures 150, 151–153 were made from the holotype, Figure 149 from a female from the Amazonas Dept., Peru.

Variation. Total length of females 11.0 to 11.4 mm.

Diagnosis. Unlike that of most *Wagneriana* species, the epigynum is longer than wide with the dorsal part of the posterior median plate swollen as seen in posterior view (bottom of Fig. 151). The epigynum is larger in size than that of *W. acrosomoides.*

Paratype. PERU *Amazonas:* Montenegro, Bagua, 350 m, 29 Sept.–1 Oct. 1963, ♀ (Herrer, P. Wygodzinsky, AMNH).

Wagneriana alma new species
Figure 154; Map 4

Holotype. Male holotype from Fazenda Almada, Uruçuca, Bahia State, Brazil, 27 Nov. 1977 (J. S. Santos), in MCN no. 15924. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace orange, darkest posteriorly with dark A-shaped thoracic mark. Legs orange with only faint rings. Venter of abdomen with white spots behind epigastric groove, black in front of spinnerets. Posterior median eyes same diameter as anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter without macroseta. Abdomen with a pair of anterior tubercles, and five tubercles at posterior end. Total length 4.8 mm. Carapace 2.3 mm long, 1.5 mm wide. First femur 2.4 mm; patella and tibia 2.6 mm; metatarsus 1.4 mm; tarsus 0.6 mm. Second patella and tibia 2.0 mm; third, 1.2 mm; fourth, 1.8 mm.

Diagnosis. The male has a large shield-shaped conductor supporting the embolus; the black shape of the embolus can be seen above the conductor (Fig. 154).

Wagneriana vegas new species
Figures 155–159; Map 4

Holotype. Female holotype and immature male paratype from Santiago de las Vegas, Cuba (Horne and Houser), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange-brown, cephalic region darker than sides with short white setae; lightest between median eyes and between lateral eyes. Legs light orange with brown rings. Venter of abdomen black. Carapace without macrosetae. Posterior median eyes 1.1 diameters of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.9 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 or more shrivelled and difficult to distinguish tubercles (Fig. 158). Total length 5.0 mm. Carapace 2.0 mm long, 1.8 mm wide. First femur 2.3 mm; patella and tibia 2.5 mm; metatarsus 1.3 mm; tarsus 0.5 mm. Second patella and tibia 2.2 mm; third, 1.3 mm; fourth, 1.9 mm.

Male from Dominican Republic. Color as in female, but cephalic region lighter than thoracic region. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.5 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes slightly less than their diameter apart. Fourth trochanter with one short macroseta. Abdomen with long tail. Total length 4.5 mm. Carapace 2.2 mm long; 1.8 mm wide. First femur 2.3 mm; patella and tibia 2.7 mm; metatarsus 1.3 mm; tarsus 0.6 mm. Second patella and tibia 2.2 mm; third, 1.3 mm; fourth, 1.9 mm.

Note. Banks considered this female specimen from Cuba to be *W. tauricornis.*

Variation. The median plate in posterior view of the epigynum is wider dorsally in specimens from Hispaniola than in the one illustrated from Cuba (Fig. 156). Total length of females 5.0 to 6.7 mm.

Diagnosis. In posterior view of the epigynum the median plate is almost circular and contains a median groove (Fig. 156). The male palpus has a short small embolus (center of Fig. 159) and a median apophysis with a distal, fleshy hook (Fig. 159).

Natural History. The male was collected from a broad-leaf and pine forest.

Distribution. Cuba, Hispaniola (Map 4).

Paratypes. DOMINICAN REPUBLIC *La Vega Prov.:* above Ciénago on "Mount Llano", 19°04'N, 70°51'W, 10 Jan. 1986, 2♀ (S. Larcher, D. Pérez, USNM); A. Bermudez Natl. Park, 10 Jan. 1986, ♂ (S. Larcher, USNM). *La Romana:* Isla Saona, Catuano, 27 Jan. 1980, ♀ (Marcano F., MNSD).

Wagneriana acrosomoides (Mello-Leitão), new combination
Figures 160–164; Map 4

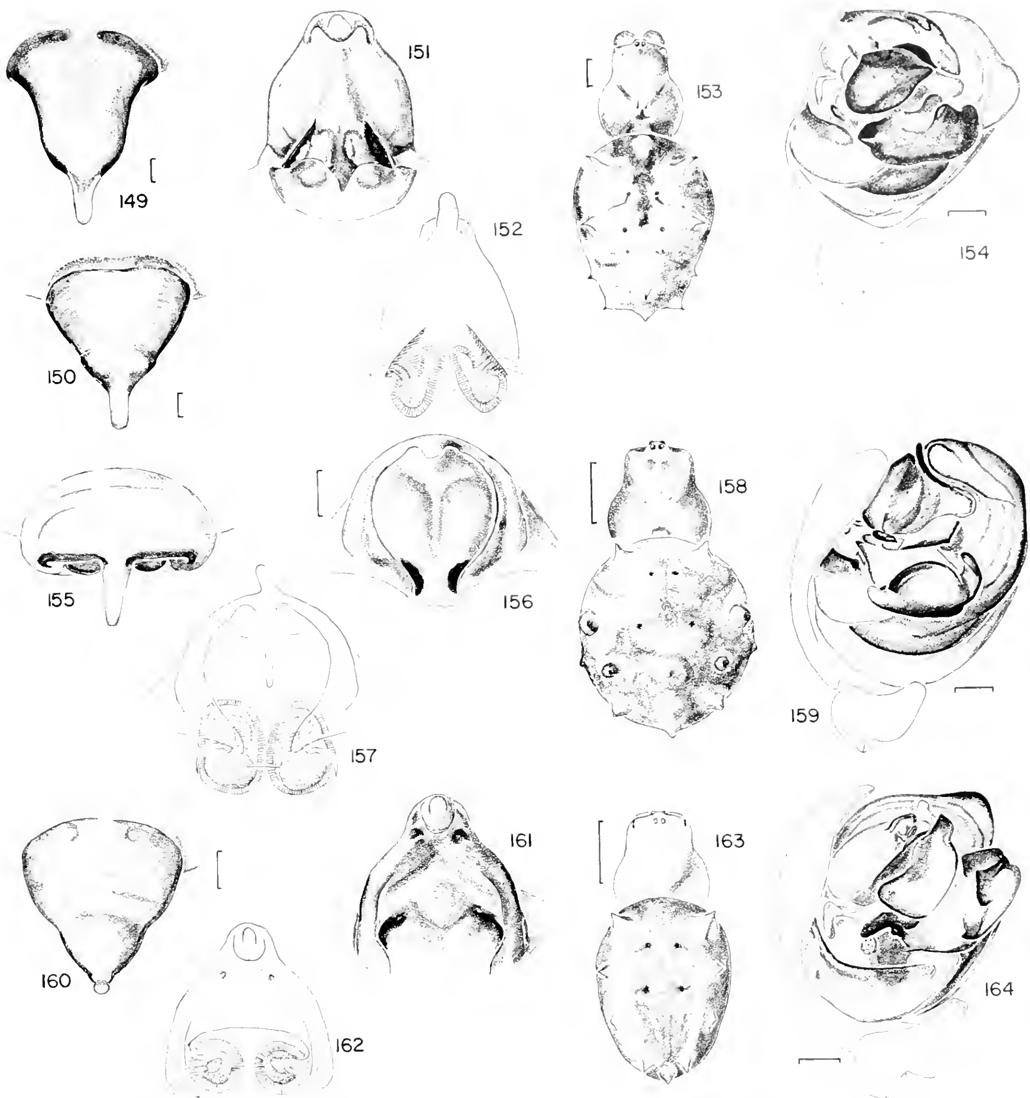
Wixia acrosomoides Mello-Leitão, 1939b: 109, figs. 9–11, ♀. Female holotype from Mazaruni Settlement, Guyana, prey of *Trypoxylon* wasp, in BMNH, examined. Roewer, 1942: 881. Bonnet, 1959: 4828.

Paraverrucosa octospinosa Mello-Leitão, 1949: 9, figs. 8–9, ♂. Male holotype from Mato Grosso, in MNRJ, examined. Brignoli, 1983: 278. NEW SYNONYMY.

Note. The abdomen, with the attached epigynum, is separate from the prosoma of the holotype of *W. acrosomoides* but they probably belong together.

Description. Female from Depto. Meta, Colombia. Carapace orange, sides of thoracic region darker. Legs orange without rings. Venter of abdomen black with a pair of white patches. Carapace without macrosetae. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.2 diameters apart. Abdomen with 9 tubercles, the third pair indistinct (Fig. 163). Total length 4.5 mm. Carapace 2.1 mm long, 1.6 mm wide. First femur 1.8 mm; patella and tibia 2.2 mm; metatarsus 1.1 mm; tarsus 0.5 mm. Second patella and tibia 1.8 mm; third, 1.1 mm; fourth, 1.7 mm.

Male from Meta, Colombia. Color as in female but abdomen lighter. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 1.4 diameters apart. Fourth trochanter with two short macrosetae. Abdomen as in female. Total length 3.7 mm. Carapace 1.9 mm long, 1.6 mm wide. First



Figures 149–153. *Wagneriana huanca* n. sp., female. 149, 150. Epigynum, ventral. 151. Epigynum, posterior. 152. Epigynum, cleared. 153. Dorsal.

Figure 154. *W. alma* n. sp., male left palpus.

Figures 155–159. *W. vegas* n. sp. 155–158. Female. 155. Epigynum, ventral. 156. Epigynum, posterior. 157. Epigynum, cleared. 158. Dorsal. 159. Male palpus.

Figures 160–164. *W. acrosomoides* (Mello-Leitão). 160–163. Female. 160. Epigynum, ventral. 161. Epigynum, posterior. 162. Epigynum, cleared. 163. Dorsal. 164. Male palpus.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

femur 1.8 mm; patella and tibia 2.1 mm; metatarsus 1.1 mm; tarsus 0.5 mm. Second patella and tibia 1.7 mm; third, 1.1 mm; fourth, 1.5 mm.

Illustrations. The illustrations were made from specimens from Meta Dept., Colombia.

Variation. Total length of females 4.5 to 5.8 mm, of males 3.7 to 3.8.

Diagnosis. The epigynum is slightly longer than wide, pointed and distally swollen (Fig. 160). In posterior view it has a ventral depression and a dorsal pair of bulges (Fig. 161). The palpus of the male has a characteristically shaped flat conductor in the middle of the palpus, and a median apophysis with a median "vertical" keel (Fig. 164).

Natural History. Females have been collected in campo grassland in Mato Grosso State. The specimens from near Manaus, Brazil, came from a wasp nest.

Distribution. Guianas and Amazon drainage (Map 4).

Records. COLOMBIA *Meta:* 20 km N Río Muco, 20 km S El Porvenir, Finca Cheneva, 170 m, 1978, 7♀, ♂ (W. Eberhard 1337, 1367, 1378, 1388, 1389, 1394, MCZ). GUYANA Kaieteur, 31 July 1911, ♀, ♂ (F. Lutz, AMNH). BRAZIL *Amapá:* Oiapoque, May 1959, ♀, ♂ (M. Alvarenga, AMNH). *Roraima:* Ilha de Maracá, 20, 25 July 1987, 3♀ (A. A. Lise, MCN). *Amazonas:* Manaus, 2♀ (M.V. Bastos Garcia, INPA). *Goiás:* Santa Isabel, Ilhado Bananal, Rio Araguaia, 15–29 July 1957, ♂ (B. Malkin, AMNH). *Mato Grosso:* 260 km N Xavantina, 400 m, 12°49'S, 51°46'W, Feb.–Apr. 1969, ♀ (Oxford Xavantina Cach. Exped., MCZ).

Wagneriana tayos new species
Figures 165–171; Map 4

Holotype. Female holotype and male paratype from Los Tayos, 3°06'S, 76°12'W (as 78°12'W in error on label), Morona-Santiago Prov., Ecuador, 24 July 1976, cliffs by stream-bed near main cave entrance (N. Engler), in MCZ. The specific name is a noun in apposition after the type locality.

Note: The latitude and longitude on the label is a Peruvian locality, a misprint.

Description. Female holotype. Carapace brown, darkest on sides of thoracic region, white setae on cephalic region. Legs light brown with darker rings. Venter of abdomen with black square constricted by a pair of white spots in front of spinnerets (Fig. 169). Carapace without macrosetae. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with four pairs of lateral tubercles and two posterior median ones (Fig. 168). Total length 7.0 mm. Carapace 2.6 mm long, 1.8 mm wide. First femur 2.5 mm; patella and tibia 2.8 mm; metatarsus 1.6 mm; tarsus 0.6 mm. Second patella and tibia 2.4 mm; third, 1.3 mm; fourth, 2.1 mm.

Male collected with female. Color as in female. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes slightly less than one diameter apart. Posterior median eyes 1.2 diameters apart. Fourth trochanter with one short macroseta. Abdomen as in female (Fig. 171). Total length 5.3 mm. Carapace 2.5 mm long; 1.8 mm wide. First femur 2.5 mm; patella and tibia 3.0 mm; metatarsus 1.7 mm; tarsus 0.6 mm. Second patella and tibia 2.3 mm; third, 1.5 mm; fourth, 2.2 mm.

Illustrations. The illustrations were made from the holotype and the male paratype collected with it.

Variation. The terminal apophysis of the male collected at Tambopata differs considerably, but other sclerites of the palpus are as in the paratype illustrated. Total length of females 5.6 to 7.0 mm.

→

Figures 165–171. *Wagneriana tayos* n. sp. 165–169. Female. 165. Epigynum, ventral. 166. Epigynum, posterior. 167. Epigynum, cleared. 168. Dorsal. 169. Abdomen, ventral. 170, 171. Male. 170. Left palpus. 171. Dorsal.

Figures 172–175. *W. yacuma* n. sp., female. 172. Epigynum, ventral. 173. Epigynum, posterior. 174. Epigynum, cleared. 175. Dorsal.

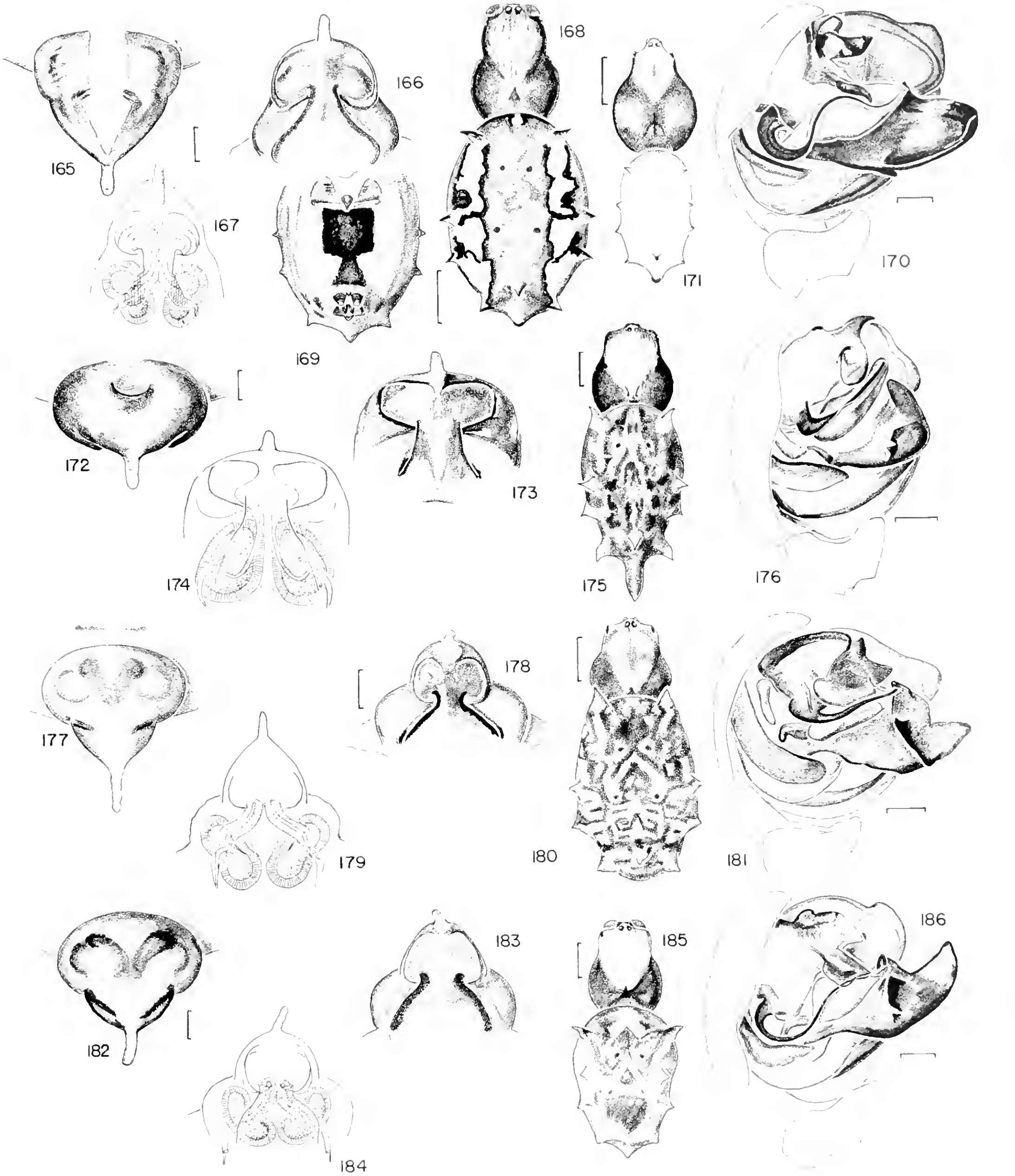


Figure 176. *W. eldorado* n. sp., male palpus.

Figures 177–181. *W. hassleri* n. sp. 177–180. Female. 177. Epigynum, ventral. 178. Epigynum, posterior. 179. Epigynum, cleared. 180. Dorsal. 181. Male palpus.

Figures 182–186. *W. silvae* n. sp. 182–185. Female. 182. Epigynum, ventral. 183. Epigynum, posterior. 184. Epigynum, cleared. 185. Dorsal. 186. Male palpus.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

Diagnosis. The posterior view of the epigynum of the female differs from that of *W. acrosomoides* (Fig. 161) by having a neck in the middle of the median plate (Fig. 166); in the cleared epigynum the connecting ducts are long with a loop at the ventral end (Fig. 167). The male differs by the long, slender, gracefully curved embolus in the palpus and by lacking the "vertical" keel on the median apophysis (Fig. 170) present in *W. silvae* (Fig. 186).

Natural History. A hot air balloon (Radeau des Cîmes) was used to collect the male from a forest canopy in French Guiana.

Distribution. French Guiana, Colombia to southern Peru (Map 4).

Paratypes. FRENCH GUIANA Petit Saut, 5°07'N, 53°05'W, Oct. 1989, ♂ (E. Nancé, MCZ). COLOMBIA *Antioquia:* Remedios, Hacienda San Martín, 87 m, 23 Dec. 1984, ♀ (M. A. Serna, MHNMC). ECUADOR *Pastaza:* Puyo, 900 m, Mar. 1941, ♀ (W. Clarke-Macintyre, AMNH). PERU *Amazonas:* Alto Río Comaina, Puesto de Vigilancia, 850–1,100 m, 21 Oct.–3 Nov. 1987, 2♀ (D. Silva D., MHNSM). *Pasco:* Huancabamba, Quebrada Castillo, NW Iscazacin, 245 m, 10°10'S, 75°15'W, 13 Sept. 1987, ♀ (D. Silva D., MHNSM). *Madre de Dios:* Tambopata Reserve, Río Tambopata, Explorers Inn, 30 Mar. 1988, 2♀, ♂ (J. Palmer, D. Smith, MCZ).

Wagneriana yacuma new species
Figures 172–175; Map 4

Holotype. Female holotype from Espíritu, Río Yacuma, Depto. El Beni, Bolivia, in vegetation, 15 April 1954 (W. Forster and O. Schindler), in ZSM. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace brown-black, center of cephalic region orange with white setae. Legs dusky orange with blackish rings. Venter of abdomen with indistinct white pigment square enclosing black pigment anteriorly, sides brown and black. Carapace with two macrosetae; thoracic depression a deep round pit (Fig. 175). Posterior median eyes same diameter as anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles (Fig. 175). Total length 7.5 mm. Carapace 2.6 mm long, 2.1 mm wide. First femur 2.7 mm; patella and tibia 3.2 mm; metatarsus 1.6 mm; tarsus 0.7 mm. Second patella and tibia 2.9 mm; third, 1.6 mm; fourth, 2.5 mm.

Diagnosis. The epigynum of this species differs from all other *Wagneriana* species by having a transverse notch anteriorly on its ventral surface (Fig. 172), resembling that of *Alpaida* species.

Paratype. A female paratype from the type locality collected on 16 April 1954 (ZSM).

Doubtful record. BRAZIL *Mato Grosso:* São Félix, 8 Apr. 1961, ♀ (AMNH).

Wagneriana eldorado new species
Figure 176; Map 4

Holotype. Male holotype from Eldorado, Misiones Prov., Argentina, Nov. 1970 (M. E. Galiano), in MACN no. 8792. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Cephalic region yellowish, thoracic region blackish brown. Legs yellowish with some narrow dark rings. Venter of abdomen mostly black with a white line on each side. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter of anterior medians. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter without macroseta. Abdomen with only indications of tubercles. Total length 3.8 mm. Carapace 1.9 mm long, 1.5 mm wide. First legs lost. Second patella and tibia 1.8 mm; third, 1.1 mm; fourth, 1.7 mm.

Diagnosis. This species differs from *W. hassleri* by having differently shaped median and terminal apophyses (Fig. 176).

Wagneriana hassleri new species
Figures 177–181; Map 4

Holotype. Male holotype from Rapununi River, near Mt. Makarapan, Rupununi County, Guyana, 5 Oct.

1937 (W. G. Hassler), in AMNH. The species is named after the collector.

Description. Female from Kuyuwini River. Carapace orange and dark brown. Legs orange with brown rings. Venter of abdomen with a black square behind epigynum, a white line on each side, and white pigment between black area and spinnerets. Carapace without macrosetae. Posterior median eyes same diameter as anterior medians, anterior laterals 0.9 diameter of anterior medians, posterior 0.8 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Abdomen with 4 pairs of tubercles and two posterior median ones, the second one small (Fig. 180). Total length 6.3 mm. Carapace 2.8 mm long, 2.1 mm wide. First femur 2.7 mm; patella and tibia 3.2 mm; metatarsus 1.9 mm; tarsus 0.8 mm. Second patella and tibia 2.7 mm; third, 1.5 mm; fourth, 2.5 mm.

Male holotype. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.5 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with one small, short macroseta. Abdomen as in female. Total length 4.0 mm. Carapace 2.1 mm long, 1.5 mm wide. First femur 2.1 mm, other articles broken off. Second patella and tibia 1.9 mm; third, 1.1 mm; fourth, 1.6 mm.

Illustrations. The illustrations were made from the male holotype and female paratype from Guyana.

Note. Males and females have not been collected together. Determination labels by di Caporiacco with the specimens from Kuyuwini had the female named *W. undecimaculata* and the male *tauricornis*. The trochanter macrosetae are broken off in the holotype but present in the paratype.

Variation. Total length of males 4.0 to 4.2 mm.

Diagnosis. In posterior view of the epigynum the females differ from *W. silvae* (Fig. 183) by having the neck of the median plate narrower (Fig. 178). The male palpus has both the embolus and median apophysis shorter (Fig. 181) than in *W. silvae* (Fig. 186).

Natural History. The specimen from Ukurua River was collected in a forest savanna.

Distribution: Guyana, lower Amazon area (Map 4).

Paratypes. GUYANA *Rupununi:* Kuyuwini Lodge, Kuyuwini River, 20 Nov. 1937, ♀, ♂ (W. G. Hassler, AMNH). *Berbice:* Canje, Ukurua Rivers, ♂ (G. Bentley, AMNH). BRAZIL *Pará:* Belém, Fazenda Velha, July 1970, ♂ (M. E. Galiano, MEG).

Wagneriana silvae new species
Figures 182–186; Map 4

Holotype. Male holotype from Puesto de Vigilancia, Pakitza, Zona Reservada de Manu Depto., Madre de Dios, 11°58′S, 71°18′W, Peru, night collecting, 2 Oct. 1987 (D. Silva D., J. Coddington), in USNM. The species is named after the collector Diana Silva D.

Description. Female from Zona Reservada de Tambopata, Peru. Carapace dark brown, cephalic region orange. Legs yellow with dusky rings. Venter of abdomen with a dusky square. Carapace without macrosetae. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter of anterior medians. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles (Fig. 185). Total length 6.5 mm. Carapace 2.9 mm long, 2.0 mm wide. First femur 2.7 mm; patella and tibia 3.2 mm; metatarsus 1.7 mm; tarsus 0.8 mm. Second patella and tibia 2.7 mm; third, 1.5 mm; fourth, 2.4 mm.

Male holotype. Color as in female but carapace brown with eye region orange and a posterior orange triangular mark pointing posteriorly on cephalic region. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.4 diameter apart. Posterior median eyes 0.8 diameter apart. Fourth trochanter with one macroseta. Total length 5.0 mm. Carapace 2.5 mm long, 1.8 mm wide. First femur 2.5 mm; patella and tibia 2.8 mm; metatarsus 1.5 mm; tar-

sus 0.7 mm. Second patella and tibia 2.2 mm; third, 1.3 mm; fourth, 2.0 mm.

Illustrations. The illustrations were made from the holotype and specimens from the Tambopata Reserve.

Variation. Total length of females 6.2 to 7.3 mm, of males 4.4 to 5.0.

Diagnosis. The female is difficult to separate from that of *W. hassleri* found in Guyana (Fig. 178). It may differ in posterior view of the epigynum by having the neck of the posterior plate wider (Fig. 183), but it is not certain that this difference is present in all females. The male differs from *W. hassleri* by having both a longer embolus and a longer median apophysis (Fig. 186), from *W. tayos* by having a "vertical" keel on the median apophysis (Fig. 186).

Distribution: Amazon drainage, Peru to Bolivia (Map 4).

Paratypes. PERU *Ucayali:* Colonia Callaria, Río Callaria, 15 km from Ucayali, Oct. 1961, ♀ (B. Malkin, AMNH). *Huánuco:* Cucharas, Huallaga Valley, Feb.–Apr. 1954, 2♀, ♂ (F. Woytkowski, CAS); Dantas to La Molina, SW Puerto Inca, 270 m, 18 May–1 June 1987, 6♀ (D. Silva D., MNHSM). *Pasco:* Huancabamba, Quebrada Castillo, NW Iscozacin, 10°10′S, 75°15′W, 1 Nov. 1986, 2♀ (D. Silva D., MHNSM). *Madre de Dios:* Zona Reservada Tambopata, common (D. Silva D., MHNSM); 15 km E Puerto Maldonado, June 1983, 2♀ (G. C. Hunter, CAS); Zona Reservada Manu, Pakitza, 2–4 Oct. 1987, ♀, ♂ (D. Silva D., J. H. Coddington, USNM). BOLIVIA *Beni:* Est. Biologica Beni, 10 Sept. 1987, ♂ (J. Coddington, USNM).

Wagneriana roraima new species
Figures 187–190; Map 4

Holotype. Female holotype and one female paratype from Ilha do Maracá, Roraima Territory, Brazil, 29 July 1987 (A. A. Lise). Holotype in MCN no. 19655, paratype in MCN no. 18808. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Cephalic region orange with some white setae, sides of thoracic region brown-black. Legs yellowish with brown rings. Venter of abdomen with black square behind epigynum, on each side of square a white line ending in a white spot in front of spinnerets. Carapace without macrosetae. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter of anterior medians. Anterior median eyes 0.8 diameter apart. Posterior median eyes 0.8 diameter apart. Abdomen with 10 tubercles, most posterior tubercles missing (Fig. 190). Total length 6.5 mm. Carapace 2.7 mm long, 2.2 mm wide. First femur 2.9 mm; patella and tibia 3.4 mm; metatarsus 1.9 mm; tarsus 0.8 mm. Second patella and tibia 2.9 mm; third, 1.6 mm; fourth, 2.5 mm.

Diagnosis. In ventral view the epigynum appears triangular (Fig. 187) and in posterior view the median plate has a neck (Fig. 188) as in *W. hassleri* (Fig. 178).

Wagneriana tauricornis (O.P.-Cambridge)
Figures 191–195; Map 4

Epeira tauricornis O. P.-Cambridge, 1889: 44, pl. 6, figs. 2, 3, ♀, ♂. Many syntype specimens from numerous localities in Guatemala and Chiriquí Prov., Panama, in BMNH, examined. Keyserling, 1892: 90, pl. 4, fig. 68, ♂.

Epeira guatemalensis O. P.-Cambridge, 1889: 40, pl. 7, fig. 8, ♂ (not ♀). Male syntypes from numerous localities in Guatemala. First synonymized by F. P.-Cambridge, 1904: 498.

Wagneria tauricornis:—McCook, 1894: 204, pl. 13, figs. 1, 2 , ♀, ♂.

Wagneriana tauricornis:—F. P.-Cambridge, 1904: 498, pl. 47, figs. 14, 15, ♀, ♂. Roewer, 1942: 881. Bonnet, 1959: 4803. Levi, 1976: 370, figs. 57–73, ♀, ♂.

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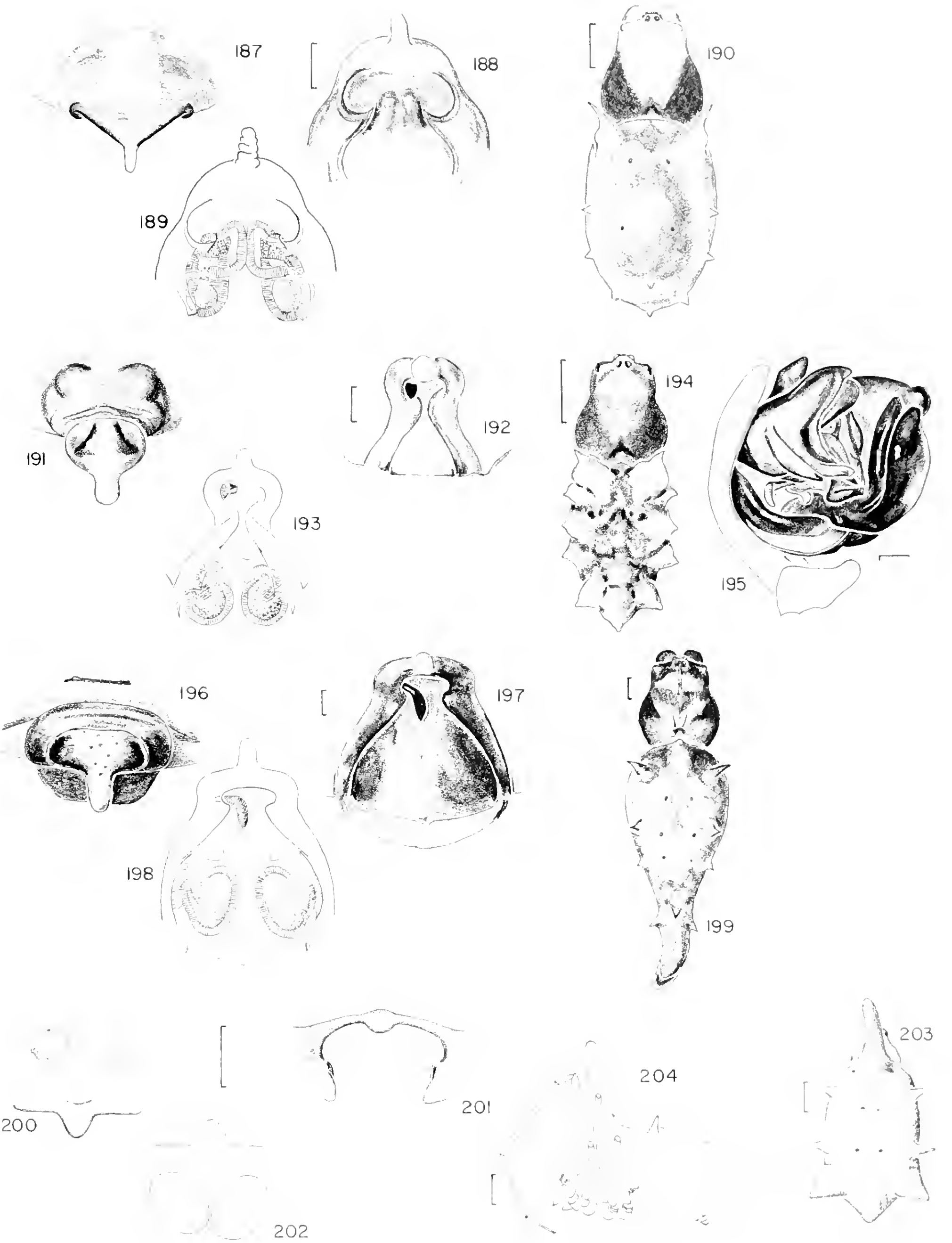
Figures 187–190. *Wagneriana roraima* n. sp., female. 187. Epigynum, ventral. 188. Epigynum, posterior. 189. Epigynum, cleared. 190. Dorsal.

Figures 191–195. *W. tauricornis* (O. P.-Cambridge). 191–194. Female. 191. Epigynum, ventral. 192. Epigynum, posterior. 193. Epigynum, cleared. 194. Dorsal. 195. Left male palpus.



Figures 196–199. *W. pakitza* n. sp., female. 196. Epigynum, ventral. 197. Epigynum, posterior. 198. Epigynum, cleared. 199. Dorsal.

Figures 200–204. *W. turrigera* Schenkel, female. 200. Epigynum, ventral. 201. Epigynum, posterior. 202. Epigynum, cleared. 203. Dorsal. 204. lateral.

Scale lines. 1.0 mm, genitalia, 0.1 mm.

Description. Female from Veracruz, Mexico. Carapace orange to dark brown, darkest on sides of thoracic region. Legs orange with brown to black rings. Venter of abdomen with indistinct paired white patches. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter of anterior medians. Anterior median eyes their diameter apart. Posterior median eyes 1.5 diameters apart. Abdomen with five pairs of tubercles and three posterior median tubercles (Fig. 194). Total length 5.0 mm. Carapace 2.3 mm long, 1.5 mm wide. First femur 2.1 mm; patella and tibia 2.4 mm; metatarsus 1.3 mm; tarsus 0.5 mm. Second patella and tibia 2.1 mm; third, 1.2 mm; fourth, 1.9 mm.

Male from Veracruz, Mexico. Color as in female. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.4 diameter apart. Posterior median eyes 1.2 diameters apart. Fourth trochanter with one short macroseta. Abdomen as in female. Total length 4.2 mm. Carapace 2.1 mm long, 1.7 mm wide. First femur 2.3 mm; patella and tibia 2.5 mm; metatarsus 1.3 mm; tarsus 0.5 mm. Second patella and tibia 1.8 mm; third, 1.3 mm; fourth, 1.8 mm.

Illustrations. The illustrations were made from specimens from Veracruz State, Mexico.

Variation. Total length of females 4.5 to 6.7 mm, of males 3.8 to 4.9.

Diagnosis. In posterior view the epigynum differs from that of other species by having a neck (Fig. 192), and it differs from that of *W. pakitza* (Fig. 197) by its proportions and by lacking macrosetae on the carapace (Fig. 194). The palpus of the male differs from that of other species by having a whale-shaped "vertical" median apophysis (Fig. 195).

Natural History. The species is commonly collected by the edge of a sweeping forest and has been collected from a palm forest in Quintana Roo State, Mexico, a tropical wet forest and a cloud forest in Costa Rica, and from leaves of agave in Colombia.

Distribution. Florida, Gulf States of United States, Mexico to Venezuela and northern Peru (Map 4).

Additional records. MEXICO *Tamaulipas:* nr. Gomez Farias (MCZ). *San Luis Potosí:* Xilitla (MCZ); Huichichuayan (AMNH); Valles (AMNH); Tamazunchale (AMNH). *Nayarit:* San Blas (MCZ); Tepic (AMNH). *Veracruz:* 40 km NW Alvarado (REL); Papantla (AMNH); Catemaco [Playa Azul] (AMNH); Fortín de las Flores (AMNH, REL); Atoyac (AMNH); Acayuca (AMNH); nr. La Palma (MCZ); Tampico (USNM). *Hildalgo:* 20 km NE Tlanchinol, 760 m (MCZ). *Oaxaca:* Soyaltepec (AMNH). *Yucatan:* 3 km E Chichen Itza (MCZ); Colonia Yucatan (AMNH). *Quintana Roo:* Kohunlich ruins, 18°26′N, 88°48′W (MCZ); Cozumel (AMNH). *Chiapas:* Palenque ruins (MCZ, AMNH); Escuintla (MCZ); Selva de Ocote, 32 km NW Ocozocoautla (CAS). GUATEMALA Nueva Concepción (CAS). HONDURAS Lago de Yojoa, 600–650 m (AMNH); Lancetillo (MCZ). NICARAGUA San Marcos (MCZ). COSTA RICA *Heredia:* La Selva (MCZ, USNM); 1 km N Montana Azul, 1,500 m (DU); NE San Rafael, 1,400 m (MCZ). *Alajuela:* San Mateo, Higuito (USNM). *Limón:* 5.5 km E Guápiles (DU); Hamburg Farm (NHMW). *Cartago:* Turrialba, (CAS). *Guanacaste:* Carrillo (MCZ). *Puntarenas:* nr. Tarcoles, 20–50 m (MCZ); Las Cruces (MCZ); Corcovado Natl. Park (MCZ); Osa Peninsula (MCZ). *San José:* Bajo La Hondura, 1,360 m, 1,600 m (MCZ); San Pedro (MCZ); San José (AMNH). *Cartago:* Cartago (AMNH, MCZ); Turrialba (AMNH, MCZ); San Isidro General (MCZ). PANAMA *Chiriquí:* Volcán (MCZ); trocha Dir. Continental, Carret. Fortuna to Chiriquí Grande (MIUP). *Coclé:* El Valle (AMNH). *Colon-Panamá:* Panama Canal area, very common (AMNH, MCZ, MIUP). BAHAMA ISLANDS: Nassau (AMNH). HAITI Port au Prince (MCZ). JAMAICA very common (AMNH, MCZ). VENEZUELA *Miranda:* Guatopo Natl. Park, Santa Cruzita, 450 m (USNM). *Carabobo:* Golfo Triste (AMNH). *Aragua:* Rancho Grande (AMNH). COLOMBIA *Magda-*

lena: San Pedro, 1,400 m (JAK); Serra Nueva Granada, 1,300 m (JAK). *Antioquia:* Guarne, 2,000 m (MCZ); San Vincente (MHNM). *Valle:* Anchicaya, 400 m, common (MCZ). ECUADOR *Pichincha:* nr. La Palma (MCZ); Tinalandia, 12 km E Santo Domingo de los Colorados, 750 m (FSCA); km 113, via Pto. Quito (MECN). *Los Ríos:* Est. Cient., P. F. Davila, Jauneche (MECN); Montalvo (AMNH). *Bolivar:* Balzapamba (MCZ, AMNH). PERU *Tumbes:* Palmal [?] (PAN); Lechugal (PAN).

Wagneriana pakitza new species
Figures 196–199; Map 4

Holotype. Female holotype from Zona Reservada Pakitza Depto., Madre de Dios, Peru, 11°58′S, 71°18′W, 3, 4 Oct. 1987 (J. Coddington, D. Silva D.), in MHNSM. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange-yellow and brown-black with two patches of dense white, thin setae. Legs orange-yellow, ringed dark brown. Venter of abdomen with some indistinct white pigment in center. Carapace with two macrosetae (Fig. 199). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. The laterals are separated by their diameter. Abdomen with four pairs of lateral tubercles and three posterior median ones (Fig. 199). Total length 14.5 mm. Carapace 3.9 mm long, 2.9 mm wide. First femur 4.7 mm; patella and tibia 5.6 mm; metatarsus 2.9 mm; tarsus 1.1 mm. Second patella and tibia 4.7 mm; third, 2.6 mm; fourth, 4.0 mm.

Diagnosis. Wagneriana pakitza is larger than *W. tauricornis*. The carapace of *W. pakitza* has a pair of macrosetae (Fig. 199) unlike that of *W. tauricornis* (Fig. 194). The epigynum resembles that of *W. tauricornis*, but differing by lacking the two black marks of the tip in ventral view (Fig. 196). In posterior view the neck of the epigynum of *W. pakitza* is near the ventral tip (top of Fig. 197), while that of *W. tauricornis* is closer to the middle (Fig. 192).

Wagneriana turrigera Schenkel
Figures 200–204; Map 4

Wagneriana turrigera Schenkel, 1953: 24, fig. 22, ♀. Female holotype from El Pozon, Falcon Prov., Venezuela, in NMB, examined. Brignoli, 1983: 281.

Note. Schenkel placed a question mark before the name of the genus in the original description.

Description. Female holotype. Carapace, legs light brown. Dorsum of abdomen yellow-white (Fig. 203); venter dusky. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen as in Figures 203, 204. Total length 6.0 mm. Carapace 2.0 mm long, 1 5 mm wide. First femur 2.5 mm; patella and tibia 3.2 mm; metatarsus 2 mm; tarsus 0.8 mm. Second patella and tibia 2.5 mm; third, 1.7 mm; fourth, 2.5 mm (after Schenkel).

Note. This is the only species with a median anterior hump that is drawn out into a tube (Figs. 203, 204). It may not belong to *Wagneriana*. It was first thought to be an immature *Wixia*; however, seminal receptacles are present. The holotype may be a penultimate instar female ready to molt.

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THE CLASSIFICATION OF THE NATICIDAE (MOLLUSCA: GASTROPODA): REVIEW AND ANALYSIS OF THE SUPRASPECIFIC TAXA

ALAN R. KABAT[1]

ABSTRACT. This paper provides a critical analysis of the 25 family level names and the 253 genera and subgenera in the gastropod family Naticidae (Prosobranchia). My systematic conclusions are based upon reexamination of the relevant type species and original descriptions, along with subsequent interpretations of the various taxa, Recent and fossil. Of the 25 family level names, 6 are here considered valid and the remainder synonyms. For the 253 genus level taxa, 65 are nomenclaturally available and in current usage; 56 are known junior synonyms; 10 are junior homonyms; 14 are *nomina nuda;* 59 are errors or emendations; and 4 are indeterminate and herein rejected as *nomina dubia*. An additional 45 genera, originally described in the Naticidae (or based on "naticid" species), are referred to various other gastropod families. An historical review of the classification of this family is presented.

INTRODUCTION

This research is preliminary to a comprehensive reclassification of the Naticidae. The ultimate goal of a classification is a complete hierarchy into which each species can be placed, with the appropriate genus and family level names fully elaborated. Traditionally, systematists used the "top-down" approach of evolutionary classification, in which the categories were subdivided, starting at the highest level and proceeding down to the species. More recently, cladistic approaches emphasize the "bottom-up" approach in which one first starts with a cladogram of the species (or sometimes genera, instead) and then determines the proper ordering and ranking of the higher categories. However, the latter approach not only requires a comprehensive understanding of all the species, but also has difficulty in dealing with fossil taxa of different time periods. That is, while depicting contemporaneous "sister taxa," it has methodological and epistemological problems in incorporating ancestor-descendant relationships.

In any event, since there are over 2,700 described species (fossil and Recent) of Naticidae, it is unlikely (if ever) that the species level nomenclature of this family will be fully rectified for the preparation of a complete classification. Furthermore, although eventually we will know the characters and relationships of the approximately 200 valid Recent species, it will not be possible to reconstruct the complete fossil history of this family. Even though the naticids, living in a sedimentary habitat, have perhaps the best fossilization potential among the Gastropoda, there are still large gaps in their fossil record—both temporally and geographically. The characters available from the fossils are, of necessity, more limited than those that are available for the Recent species. Therefore, a classification of the Naticidae, including the fossils, can only be an approximation at best. While it will be reasonably satisfactory for the Recent species, as well as for some of the extinct taxa, there will be many extinct species (particularly from the Mesozoic) that will defy reconciliation with a sophisticated classification. The term

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...certae sedis" can be used to indicate taxa of unknown (or uncertain) relationships; and "*sedis mutabilis*" for taxa of interchangeable positioning (Wiley, 1981: 211). While these terms may be of some heuristic value in indicating the state of knowledge with respect to fossil taxa, they do indicate the limitations of classification with respect to fossils.

HISTORICAL REVIEW

The following chronological analysis of the major "innovations" in naticid classification starts with Aristotle and Linnaeus and proceeds to the present. This concise synopsis does not attempt to discuss every relevant publication. The emphases include critical analyses of several major problems (*e.g.*, the treatment of European fossil naticids in the early 1800s) and discussion of the comprehensive molluscan classifications.

Aristotle was the first to describe naticids; his term "Neritae" actually encompassed both naticids and hermit crabs occupying naticid shells (Aristotle, 345–342 B.C., Book 4(4):42, 43; Récluz, 1856:44–45). Linnaeus (1758) described seven species subsequently referred to the Naticidae; he placed them in the genera *Helix* and *Nerita*. The former name included a heterogeneous assemblage of marine, land, and freshwater snails; the latter name was somewhat more focused in comprising prosobranch gastropods. Specifically, he divided *Nerita* into three groups: "umbilicatae," "imperforatae labio edentulo," and "imperforatae labio dentato." The latter two groups represent the modern concept of Neritidae and the former corresponds to the Naticidae. This correlated with the pre-Linnaean work of Adanson (1757) who had separated out "Natica" from "Nerita"; however, the former name was not used by Linnaeus. Further discussion of the Linnaean species and their classification is provided by Kabat (1990).

The remaining half of the eighteenth century set the stage for several significant problems regarding naticid classification and higher level nomenclature. Scopoli (1777) was the first post-Linnaean author to validate Adanson's *Natica;* however, Lamarck (1799) was often incorrectly considered to be the source for this name by authors unaware of Scopoli. Since the type species are not congeneric, Lamarck's name is a junior homonym but not a junior synonym of *Natica* Scopoli; the name *Naticarius* Duméril, 1806 is available for "*Natica sensu* Lamarck." The generic names of Duméril have often been rejected by subsequent authors since they were originally intended to represent the "animal" (*i.e.*, "Natica" as the shell, "Naticarius" as the animal within the shell). Both generic names remain widely used and it would be misguided to reject *Naticarius* as the only other available name is *Naticus* Montfort, 1810, which has not been used by other authors. Article 17 of the *International Code of Zoological Nomenclature* (1985) clearly states that names such as those of Duméril are nomenclaturally available.

Röding (1798) provided many new names that preempted the better-known names of Lamarck's classical work (1799). Röding placed the naticid species into three genera: *Sinum, Albula,* and *Cochlis;* these genera were widely separated by Röding and he was unaware of their relationships. *Sinum* is the currently accepted name for the auriform naticids which Linnaeus had placed in *Helix* and is the basis for the subfamily Sininae. The equivalent genus *Sigaretus* Lamarck, 1799 was erected for the same species, and the latter name was widely used in the nineteenth century (Kabat, 1990:4–5). *Albula* and *Cochlis* represented a separation of the species of "Natica" (that name was not used by Röding). *Albula* corresponded to those naticids with corneous opercula and glossy shells; as a junior homonym of *Albula* Osbeck, 1762 (Pisces), it was replaced by *Polinices* Montfort, 1810 (the latter the basis for the subfamily Polinicinae). Röding's work was important in establishing this separation of the naticid species into three groups, which

today correspond to three (of four) naticid subfamilies.

Lamarck (1804) initiated a major nomenclatural controversy, involving recognition and classification of fossil naticids. The first post-Linnaean naticid described was a fossil from England (*Helix mutabilis* Solander in Brander, 1766), but the first explicit discussion of fossil naticids was with the description of Paris Basin fossils (Lamarck, 1804). He used the genus *Ampullaria* Lamarck, 1799 (originally proposed for freshwater gastropods) for twelve fossil species now attributed to the Naticidae (Lamarck, 1804:30–34). He noted that these fossils could be confounded with those of true naticids but maintained their identity as ampullariids. This was questioned by Deshayes (1838:528–529) who concluded that ". . . aussi Lamarck commit plusieurs erreurs en comprenant dans son genre des espèces fossiles . . ." and thought they were more likely to be naticids; this is corroborated by the presence of fossils of other marine taxa.

Bowdich (1822) erected *Ampullina* for these marine fossils and restricted *Ampullaria* to the freshwater shells. Bowdich's name was often misinterpreted, as his illustration was poor; however, it was significant in separating the fossil naticids from the freshwater ampullariids. Concurrently, James Sowerby (1812–22) and James de Carle Sowerby (1822–46) included descriptions of a number of fossil species of *Natica* and *Ampullaria*. It was noted (Sowerby, 1821:151; 1822:97; 1826: 40) that the fossil species placed in the latter genus should be separated from *Ampullaria sensu strictu;* and the substitute name *Globulus* was proposed (J. de C. Sowerby, 1835:246). The Sowerbys had overlooked *Ampullina* Bowdich; furthermore, *Globulus* was a junior homonym of *Globulus* Schumacher, 1817 (Trochidae).

Two authors independently recognized this problem and attempted to resolve it. The first was Agassiz (in Sowerby, 1837a,b: 14; 1839a,b:14), whose unauthorized "pirated" translations of the Sowerbys's work included a revisionary note proposing the name *Euspira* for these fossil naticids. Ironically, Agassiz (1848:437) later listed "*Euspira* Agass. Moll., 18.." since he was uncertain as to the original attribution of his own name! Swainson (1840) emended *Globulus* to *Globularia;* both replacement names have had a checkered and overlapping history, especially with regard to their type species (see the generic compilation for further discussion). The resolution is the recognition of three valid generic names for certain European (and other) Cenozoic naticids: *Ampullina*, *Euspira*, and *Globularia*. In this century, *Euspira* has been extended to cover several Recent species sometimes referred to *Lunatia* Gray, 1847. Some authors have desired to maintain the use of *Lunatia*, but that name is unquestionably a junior synonym of the obscure taxon *Laguncula* Benson, 1842. The best solution is to treat both *Laguncula* and *Lunatia* as synonyms of *Euspira*.

Throughout the rest of the nineteenth century to present times, numerous additional fossil naticid genera were described. In a few cases, some taxa were from the Paleozoic and referable to other families since the oldest naticids are from the Mesozoic. Nevertheless, we are left with a proliferation of fossil taxa which remain problematical in their placement within a comprehensive classification of the Naticidae. Usually these descriptions were not accompanied by explicit discussions of naticid classification.

The discussion and description of new Recent genera of naticids continued unabated during the 1800s. One problem included the confusion of *Sinum* and lamellariids in *Sigaretus* (=*Cryptostomus*). Both groups are superficially similar in their auriform shells, and several monographs referred lamellariids to these naticid genera (and *vice versa*); these misidentifications were discussed by Gray (1824).

The twentieth century brought noteworthy modernization to the classification of the naticids. Four works from the in-

Table 1. Classifications of the Naticidae (1925–1937). Indentations indicate subgenera and sections; misspellings are corrected herein.

Cossmann (1925:13–14, 98–99)*	Thiele (1929:259–262)	Finlay and Marwick (1937)
Euspiridae	Naticacea	Naticidae
Pictavia		
Ampullina	Naticidae	Naticinae
Megatylotus	Frovina	Natica
Deshayesia	Frovina	Naticarius
Cernina	Sublacuna	Tanea
Ampullonatica	?Elachisina	Tectonatica
Vanikoropsis	Acrybia	Taniella
Crommium	?Amaurella	Notocochlis
Amauropsella	Amauropsis	Proxiuber
Wexfordia	Acrybia	Stigmaulax
Greggsia	Polynices	Gennaeosinum
Ampullospira	Friginatica	Euspira
Amauropsis	Lunatia	Tasmatica
Euspirocrommium	Payraudeautia	Austrocochlis
Tylostoma	Naticina	Pristinacca
	Polynices	Carinacca
[Naticopsidae]	Neverita	Magnatica
[Neritopsidae]	Glossaulax	Spelaenacca
	Mammilla	Nacca
Naticidae	Propesinum	Payraudeautia
Naricopsina	Natica	
Gyrodes	Cryptonatica	Poliniceinae
Sigaretopsis	Natica	Polinices
Natica	Stigmaulax	Conuber
Nacca	Globularia	Mammilla
Stigmaulax	Sigaretus	Polinella
Neverita	Eunaticina	Neverita
Tectonatica	Heliconatica	Cepatia
Payraudeautia	Sigaretus	Eunaticina
Amauropsina	Haliotinella	Pervisinum
Polynices		Sigaretotrema
Mammilla		Sigatica
Pliconacca		Lunatia
Lunatia		Uberella
Labellinacca		Friginatica
Cepatia		Amauropsona
Sigaretus		Amauropsis
Sigaretotrema		
Eunaticina		Globisininae
		Globisinum

* The nominate subgenera and sections are not included since Cossmann always listed them first.

terregnum stand out in their comprehensive and critical approach. Cossmann's terminal volume of his compilations of fossil mollusks (1925) covered the majority of the then known fossil naticid taxa, with extensive commentary. He referred the naticids to two families, which were incongruously separated by the Paleozoic Naticopsidae and Neritopsidae (Archaeogastropoda) (Table 1). The first was the Euspiridae with six extinct genera including nine additional subgeneric and section names (Cossmann, 1925:13–14). This family is loosely equivalent to the current subfamily Ampullospirinae (Cox, 1930:170); but, as the genus *Euspira* was not included by Cossmann, one wonders why that family name was used. The second family recognized was the Naticidae, with five genera (two extant) including fourteen

additional subgeneric and section names (Cossmann, 1925:98–99). This well-illustrated work is otherwise flawed by its reliance on the generic assignments of other authors, since Cossmann could not always examine the original material. The higher standards of the earlier volumes in this series were not met because of the posthumous publication of his last volume.

Thiele's work (1929–31), although limited to the Recent taxa, represented the first thorough synthesis of conchological and anatomical information in the classification of mollusks. For the subclass Prosobranchia, he erected three orders, of which the Mesogastropoda contained 15 "Stirps" (=superfamilies), the twelfth being the monofamilial Naticacea. He thus confirmed the somewhat isolated placement of the naticids, in that no other families seemed directly related. For the Naticidae, Thiele (1929:259–262) recognized 8 genera, including 20 subgenera (Table 1).

The monograph of the early Tertiary Wangaloan fauna of New Zealand by Finlay and Marwick (1937) belies its systematic importance: there is an extensive discussion of the classification of the Naticidae (pp. 47–57), including the descriptions of six new genera. Evolutionary relationships are obscured because an overabundant nomenclature precludes comparisons with other faunas. Three subfamilies and 34 genus level taxa were recognized: Naticinae, Poliniceinae, and the monogeneric Globisininae (Table 1). Beu and Maxwell (1990) provided further discussion of some of these taxa.

Wenz (1941:1017–1045) brought together the most comprehensive compilation of fossil and Recent naticid taxa. He recognized the monofamilial superfamily Naticacea, with six subfamilies and 75 genus level taxa: Gyrodinae (extinct), Globulariinae, Polinicinae, Globisininae, Sininae, and Naticinae (Table 2). Although he synonymized numerous generic names and simplified the generic taxonomy, he could not treat critically the large number of genera described in the 1930s, so some of the names which he recognized have been (or will be) subsequently synonymized.

More recently, Taylor and Sohl (1962) presented a classification of the Gastropoda; their placement of the Naticidae essentially followed Thiele and Wenz, *i.e.*, a monofamilial superfamily between the Atlantacea and Tonnacea. Their estimate of a total of 75 genera of naticids is also from Wenz (1941). This work was radically revised by Golikov and Starobogatov (1975) who not only elevated the Aspidophora (=Naticacea) to an order, but also elevated six previously recognized subfamilies to families: Gyrodeidae, Globulariidae, Polinicidae, Sinidae, Choristidae, and Naticidae. Schileyko (1977) recognized three Recent families of naticids (Globulariidae, Polinicidae, and Naticidae, the latter including the Sininae) (Table 3). In a review of the Russian naticids, Golikov and Sirenko (1983, 1988) replaced the Aspidophora with the wholly equivalent "Order Naticiformes" (emended from "Naticata" Pchelintsev [1963: 20]). In another extreme revamping, Golikov and Starobogatov (1989:66) divided the Naticiformes into two suborders: "Globularioidei" (Golikov and Starobogatov, 1989:66, 73) and "Naticoidei" (Pchelintsev, 1963).

In contrast, we have several species level monographs which presented generic classifications in the context of their faunal treatments. It must be remembered that these authors only considered the taxa from one area and their classifications were not intended to be of the entire family. Oyama's (1969) preliminary treatment, marred by misspellings, of the Recent Japanese naticids separated the subfamily Poliniceinae into three tribes (Table 3). A more critical faunal work was that of Marincovich (1977), who monographed the Cenozoic naticids of the Eastern Pacific, reviewing a number of fossil genera; again, he was not able to make global comparisons and some of his conclusions will have to be modified. His subfamilial classification (Ampullospirinae, Polinicinae, Nati-

TABLE 2. CLASSIFICATION OF THE NATICIDAE (1941). INDENTATIONS INDICATE SUBGENERA AND SECTIONS; MISSPELLINGS ARE CORRECTED HEREIN.

Wenz (1941:1017–1045)		
Naticacea	Polinicinae	Globisininae
	Frovina	Globisinum
Naticidae	Prolacuna	
	?Elachisina	Sininae
Gyrodinae	Polinices	Sinum
Naricopsina	Glossaulax	Ectosinum
Gyrodes	Conuber	Heliconatica
Sigaretopsis	Mammilla	Haliotinella
	Polinella	
Globulariinae	Dallitesta	Naticinae
Pictavia	Pliconacca	Natica
Ampullina	Neverita	Naticarius
Ampullinopsis	Cepatia	Natella
Pseudamaura	Eunaticina	Quantonatica
?Pseudotylostoma	Pervisinum	Tanea
Globularia	Sigaretotrema	Tectonatica
?Waluia	Sigatica	Taniella
Eocernina	Lunatia	Notocochlis
Deshayesia	Uberella	Proxiuber
Nanggulania	Friginatica	Stigmaulax
?Ampullonatica	Amauropsona	Gennaeosinum
Vanikoropsis	?Billiemia	Nerinatica
Amaurellina	Bulbus	Euspira
Crommium	?Amaurella	Tasmatica
Pachycrommium	Amauropsis	Austrocochlis
Euspirocrommium	Heligmope	Pristinacca
Lacunaria	Amauropsina	Carinacca
Tylostoma	Wexfordia	Magnatica
?Stelzneria		Spelaenacca
		Nacca
		Payraudeautia

cinae, Sininae) is that which is currently used (Table 3). Majima (1989) reviewed the Cenozoic naticids of Japan; this work is of higher standards than is Oyama's, but the overall scheme remains that of Marincovich.

Recently, Kase (1990:565) confirmed that the aberrant "*Natica*" *fluctuata* Sowerby is actually referable to the Architaenioglossa; unfortunately his conclusions are affected by several misinterpretations: (1) he used *Globularia* rather than *Cernina* for this species (see the discussion of the two genera in the catalogue herein), (2) he stated that *fluctuata* was the only living species of the "family" Ampullospiridae (=Ampullospirinae)—in fact, there is also *Amauropsis* with several Recent species, and (3) since *fluctuata* was not naticid, he then extrapolated this result to conclude that all of the ampullospirine species (and genera) were also not naticid and were all to be removed from the Naticidae. Kase did not analyze the numerous described taxa (Recent and fossil) of the Ampullospirinae to determine their relationships, not did he provide any criteria by which these taxa may be differentiated as ampullospirines. By shell characters alone, *fluctuata* shows little relationship to the other ampullospirines and merely demonstrating that this species is non-naticid does not prove that the other taxa of this subfamily are also not naticids.

To summarize, starting from an initial confusion of *Natica* with *Nerita*, we have advanced to a more sophisticated modern classification. Nevertheless, divergent ap-

TABLE 3. CLASSIFICATIONS OF THE NATICIDAE (1969–1977). INDENTATIONS INDICATE SUBGENERA AND SECTIONS; MISSPELLINGS ARE CORRECTED HEREIN.

Oyama (1969:69–70)	Marincovich (1977)	Schileyko (1977)
Naticidae	Naticacea	Order Naticiformes
Globisininae	Naticidae	Superfamily Naticoidea
?Bulbus		
?Amaurella	Ampullospirinae	Globularidae
	Amauropsis	Globularia
Poliniceinae	Lacunaria	
Poliniceini	Crommium	Polinicidae
Lunatia	Eocernina	Polinices
Neverita	Ampullospira	Amauropsis
Glossaulax	Tejonia	Conuber
Polinices	Euspirocrommium	Falsilunatia
Mammilla	Pachycrommium	Frovina
	Amaurellina	Glossaulax
Eunaticini	Gyrodes	Lunatia
Eunaticina		Mammilla
Sigaretotrema	Polinicinae	Neverita
Sigatica	Polinices	Prolacuna
	Euspira	
Sinini	Hypterita	Naticidae
Sinum	Mammilla	Naticinae
Ectosinum	Neverita	Natica
	Glossaulax	Euspira
Naticinae	Calinaticina	Scarlatia
Natica	Bulbus	Tectonatica
Naticarius	Choristes	
Notocochlis		Sininae
Paratectonatica	Sininae	Sinum
Cryptonatica	Sinum	Ectosinum
Tanea	Eunaticina	Eunaticina
	Naticinae	
	Natica	
	Naticarius	
	Carinacca	
	Lunaia	
	Glyphepithema	
	Stigmaulax	
	Tectonatica	
	Cryptonatica	

proaches have been utilized, and problems with the placement of various fossil taxa remain. In particular, the status of the Triassic–Jurassic "naticids" is doubtful since they may instead be referable to the Neritoidea or to extinct Mesozoic families. As yet, there is no resolution to this problem; future research may elucidate the familial status of these early Mesozoic taxa and determine the origin of this family. Usually the family is presumed to have originated in the Triassic (Wenz, 1941), though it may prove to have arisen in the Jurassic.

FAMILY LEVEL NAMES

This section treats all the taxa proposed for the Naticidae at the family level (*i.e.*, superfamily, family, subfamily, tribe). As systematists are well aware, the dating and attribution of these names can be problematical, since the first author to use such a

name rarely indicated that it was a new name. Several relevant principles from the *International Code of Zoological Nomenclature* (1985) should be kept in mind. When a name is initially established for a certain rank, it is considered to be simultaneously established at all other family level ranks, with the same author and date (Article 36a). Additionally, if the type genus is a junior synonym, then that family name can only be replaced if there is already another, earlier family name based on the senior generic name, in order to stabilize nomenclature, unless this change in family names was made before 1961 (Article 40).

The task of compiling and analyzing these names for the Naticidae was made easier by the herculean compilation of prosobranch family level names (excluding the Archaeogastropoda) of Ponder and Warén (1988). Although not complete, their list is far more comprehensive than anything previously published. With respect to the Naticidae, I have only found a half-dozen additional relevant names. However, Ponder and Warén did not provide the page numbers or the bibliographic references, which I have included herein (Table 4). They noted (p. 301) that the name Naticidae dated from Forbes (1838), but that "there are two family group names earlier than Naticidae that appear to be valid." That is, they included "Sigaretinae Cuvier, 1817, as Sigaretina" and "Cryptosomidae Gray, 1827." Unfortunately, I was unable to find either name in the works of Cuvier or Gray, and W. Ponder and A. Warén (personal communication) have agreed that they were in error in using those names. There is a "Fam. Sigareteae" Menke, 1828, which was emended to Sigaretinae by Wiegmann (1832). In any event, the genera upon which these names are based (*i.e.*, *Sigaretus* Lamarck, 1799 and *Cryptostomus* Blainville, 1818) are both junior synonyms of *Sinum* Röding, 1798. Incidentally, there is also a "Sagaretidae" Forbes (1838:29), which is an error for Sigaretidae; however, Forbes's name was based on what are now referred to the Lamellariidae, rather than the naticid genus *Sinum* Röding, 1798. My conclusion is that, in fact, there are no valid family level names prior to the Naticidae Forbes, 1838.

Ponder and Warén (1988:301) included the family level name Tylostominae Stoliczka (1868:292). The status of the taxon *Tylostoma* (Cretaceous, Europe) remains uncertain; some species, including the type,

TABLE 4. FAMILY LEVEL NAMES OF THE NATICIDAE.

Naticoidea Forbes, 1838 (*nomen translatum*, Philippi, 1853:180 as Naticacea)
- = Choristiacea Verrill, 1882 (*n.t.* Kuroda, Habe, and Oyama, 1971:93 [62])
- = Aspidophora Fischer, 1884:652, 653
- = Gyrodesacea Wenz, 1941 (*n.t.* Pchelintsev, 1963: 20, 38)
- = Naticiformes Pchelintsev, 1963:20 (*n.t.* Naticata; Golikov and Sirenko, 1983:1334)

Naticidae Forbes, 1838:29
- ? = Praenaticinae Cossmann, 1925:98
- ? = Verenaticinae Cossmann, 1925:98
- Naticinae Forbes, 1838:29
  - = Naticina Macgillivray, 1843:4, 51, 124
- Polinicinae Gray, 1847:149 (*n.t.* Polinicina; Finlay and Marwick, 1937:53)
  - = Neveritina Gray, 1857:48
  - = Choristidae Verrill, 1882:540
  - = Mammillinae Iredale and McMichael, 1962:57
- Sininae Woodring, 1928:387
  - = Sigaretinae Menke, 1828:51 (*n.t.* Sigaretea; Wiegmann, 1832:540)
  - = Sagaretidae Forbes, 1838:29 (error; non-naticid)
  - = Globisininae Powell, 1933:168
    - = Globisiinnae Oyama, 1969:73*
    - = Golobisininae Oyama, 1969:73*
    - = Gloisininae Oyama, 1969:74*
  - = Eunaticini Oyama, 1969:70
  - = "Sigaretinae Cuvier, 1817" Ponder and Warén, 1988:301
  - = "Cryptosomidae Gray, 1827" Ponder and Warén, 1988:301
- Ampullospirinae Cox, 1930:170
  - = Euspiridae Cossmann, 1907:21 (error; not based on *Euspira* [Polinicinae])
  - = Ampullininae Cossmann in Cossmann and Peyrot, 1918:181 (error; based on incorrect type species)
  - = Gyrodinae Wenz, 1941:1017
  - = Globulariinae Wenz, 1941:1019
    - = Globulaliinae Oyama, 1969:72*

* Incorrect subsequent spelling.

may prove to be neritoidean archaeogastropods. Hence, I have omitted that name from Table 4, pending resolution of this problem. Russian authors have often divided the family Naticidae into several families within the "Order Naticiformes Pchelintsev, 1963"; discussion of these ordinal level names was covered in the preceding historical review.

GENUS LEVEL NAMES

The development of the generic nomenclature of the Naticidae is itself interesting and some details were discussed previously. Here I provide a comprehensive nomenclatural analysis of the genus level taxa. Most of these were described and used in "isolation," without a critical comparison with the other relevant, previously described genera. The result has been a proliferation of names, many of which have never been used subsequently. Correlated with this is the fact that many of the (post-1800) described naticid species were placed in three "common" naticid genera: *Natica*, *Polinices*, and *Sigaretus* [=*Sinum*] (in decreasing frequency). Also, some of the pre-1850 naticid species (especially fossils) were originally referred to the non-naticid genera *Ampullaria*, *Helix*, *Nerita*, and *Turbo*.

My original intention was to produce a fully resolved generic classification of this family. Initially, with perhaps 50 valid names, this task seemed to be straightforward. Over the last few years, this list has been more than doubled with the addition of numerous previously overlooked names. Some of these names are already known to be junior synonyms, homonyms, rejected as *nomina nuda*, or referable to other gastropod families. Yet, there are still many available fossil genera whose status I have not determined. Hence, this list is only a precursor to a full classification. This section will provide a critical basis for a modern understanding of the naticid genera, and will assist with the generic assignments of the species.

To increase the value of this list, I have included numerous annotations with respect to nomenclatural and other problems. For each genus, the type species and the method of designation is presented; synonyms or homonyms are indicated. The geological and geographical occurrence of the type species is included; usually, the genus as a whole encompasses a broader temporal and spatial range. Incidentally, I have also included the aforementioned four non-naticid genera for the reader's convenience. This list is fully cross-referenced. Further research will entail redescriptions of the valid genera and a tabulation of the known species (Recent and fossil) referable to each.

Altogether, 253 genus level names (not counting the aforementioned four non-naticid genera) are listed. Of these, 65 (=26%) are nomenclaturally available and in current usage. However, future research will undoubtedly reveal new synonymies. Additionally, 56 names (=22%), including 21 newly synonymized herein, are junior synonyms. Ten names are junior homonyms (seven since renamed). Fourteen names are *nomina nuda* or occur in rejected works. Fifty-nine names (=23%) are errors or emendations and four names are herein rejected as *nomina dubia*. Finally, 45 names (=18%) are referable to other gastropod families of which 11 are herein newly transferred. A sizable number of these names (64, or 25%) were never recorded in the *Zoological Record* and the various editions of Neave (1939–1940 ff.).

ALPHABETICAL LIST OF THE GENERA OF NATICIDAE

ACILIA Koken, 1896:110. Type species *Acilia aequalis* Koken 1896; subsequent designation Koken, 1897:83. Triassic, Europe. Originally described in the Scalidae; Diener (1926:124) placed this in the Naticidae; Wenz (1939:510) transferred this to the Lacunidae.

ACRYBIA H. and A. Adams, 1853:207. Type species *Natica flava* Gould, 1839; monotypy [=*Natica fragilis* Leach, 1819]. Recent, North Atlantic. Is a junior subjective synonym of *Bulbus* Brown in Smith, 1839 as the type species are both junior synonyms of *N. fragilis*.

ALBULA Röding, 1798:20; *non* Osbeck, 1762 (Pisces). Type species *Nerita mammilla* Linnaeus,

[17]58. Subsequent designation Winckworth, 1945: [1]37. See *Polinices* Montfort, 1810.

ALCONATICA Vaught, 1989:35. Error for *Aloconatica* Shikama, 1971.

ALOCONATICA Shikama, 1971:28. Type species *Aloconatica kushime* Shikama, 1971; monotypy. Recent, Japan. Herein treated as a junior synonym of *Stigmaulax* Mörch, 1852. Erroneously placed in the Conacea (Neogastropoda) by Vevers, *et al.* (1975: 185).

AMAULOPSIS Kotaka, 1962:134. Error for *Amauropsis* Mörch, 1857.

AMAURA Möller, 1842:80. Type species *Amaura candida* Möller, 1842; monotypy. Recent, North Atlantic. *Non Amaura* Heubner, 1837 (Lepidoptera). Gray transferred this to the Pyramidellidae and emended the name to *Amoura* Gray (1847: 160). "*Amaura* de Folin, 1873" Vaught, 1989:62; error for *Amoura* Folin, 1873 (renamed *Folinella* Dall and Bartsch, 1904) (Pyramidellidae). Some subsequently described species placed in this genus may be naticid.

AMAURELLA A. Adams, 1867:311. Type species *Macrocheilus japonicus* A. Adams, 1860; original designation. Recent, Japan. Is a junior synonym of *Microstelma* A. Adams, 1861, *fide* Ponder (1985a: 97). A. Adams had compared *Amaurella* with *Amaura* (*q.v.*); subsequently placed as a subgenus of *Acrybia* [=*Bulbus*] by Thiele (1929:260), see also Wenz (1941:1035).

AMAURELLINA Fischer, 1885 [Jan.]:766; *ex* Bayle MS. Type species *Ampullaria spirata* Lamarck, 1804; monotypy. Eocene, Europe. Synonyms include *Lupia* Conrad, 1865 and *Amauropsella* Chelot, 1885.

AMAUROPOPSIS Bonarelli, 1921:73. Error for *Amauropsis* Mörch, 1857.

AMAUROPSELLA Chelot, 1885 [post. Sept.]:202–203; *ex* Bayle MS. Type species *Ampullaria spirata* Lamarck, 1804; original designation. Eocene, Europe. Is a junior objective synonym of *Amaurellina* Fischer, 1885.

AMAUROPSINA Chelot, 1885:203; *ex* Bayle MS. Type species *Ampullaria canaliculata* Lamarck, 1804, original designation. Eocene, Europe. *Amaurospina* Sacco, 1891, error.

AMAUROPSIS Mörch, 1857:81 (9). Type species *Natica helicoides* Johnston, 1835 [=*Nerita islandica* Gmelin, 1791]; subsequent designation Dall, 1909:89. Recent, North Atlantic and Arctic. *Amauropopsis* Bonarelli, 1923; and *Amaulopsis* Kotaka, 1962, errors. *Non Amauropsis* Sharpe, 1894, error for *Anuropsis* Sharpe, 1883 (Aves). Several Antarctic species were referred to this genus by Dell (1990:139–144), who was unable to separate them from the Arctic species at the generic level.

AMAUROPSONA Finlay and Marwick, 1937:56–57. Type species *Nucleopsis major* Marshall, 1917; original designation. Paleocene, New Zealand.

AMAUROSPINA Sacco, 1891:331 (107). Error for *Amauropsina* Chelot, 1885.

AMPLOSTOMA Stoliczka, 1868:312. Type species *Amplostoma auriforme* Stoliczka, 1868; monotypy. Cretaceous, India. Tryon (1886:11) used this as a subgenus of *Sigaretus* [=*Sinum*], and Wenz (1940:880) transferred this to the Fossaridae.

AMPULELLA "Cox" Woodring, 1957:95. Error for *Ampullella* Cox, 1931.

AMPULINA Hanna, 1927:306. Error for *Ampullina* Bowdich, 1822.

AMPULLARIA Lamarck, 1799:76. Type species *Helix ampullacea* Linnaeus, 1758; monotypy. Recent, Europe. A junior objective synonym of *Pila* Röding, 1798. *Ampullaria* is a genus of freshwater prosobranch gastropods and this name was subsequently used by Lamarck (1804:30–34) and J. Sowerby (1819–1846) for fossil naticids. See the discussion under *Globulus* Sowerby, 1835 and *Euspira* Agassiz in J. Sowerby, 1837.

AMPULLELLA Cox, 1931:38. Type species *Ampullaria depressa* Lamarck, 1804; original designation. Eocene, Europe. Is a junior objective synonym of *Ampullina* Bowdich, 1822. Cox had thought that the type species of *Ampullina* was *Natica labellata* Lamarck, 1804. *Ampulella* Woodring, 1957 is a misspelling.

AMPULLINA Bowdich, 1822 (Feb.):31. No originally included species; figure was unidentified. The first subsequently included species was *Ampullaria depressa*, Lamarck, 1804 by Sowerby in Dixon, 1850:98, and is the type species [ICZN Article 69(a)(i)(1)]. Eocene, Europe. Cossmann (1888:170; 1925:18) incorrectly stated that the type was *Ampullaria sigaretina* Lamarck, 1804. As Dall (1909: 89) and Stewart (1927:330) have indicated, Bowdich's figure is of *depressa,* not *sigaretina*. Cox (1930:170; 1931:38) thought that the figure was of *Natica labellata* Lamarck, 1804. Sowerby in Dixon (1850:178–179) explicitly differentiated between *Natica*, *Ampullina*, and *Globularia*. *Ampullella* Cox, 1930 is a synonym. "*Ampulline* Lam." of Defrance, 1821 and "*Ampullina* Lam." of Férussac, 1822 and of Deshayes, 1830 are *nomina nuda*. *Ampulina* Hanna, 1927 is an error for *Ampullina* Bowdich, 1822. *Ampullina* Blainville, 1824 is *Eutrochatella* Fischer, 1885 (Helicinidae). *Ampullina* Guppy, 1895 is *Oxyrhombus* Crosse and Fischer, 1893 (Helicinidae); see Clench and Jacobson (1966: 71, 1968:9).

AMPULLINA "Lamarck" Férussac, 1822 (13 April): xxxiv. *Nomen nudum;* published in synonymy of *Natica* (Kennard, 1942b:112). *Non Ampullina* Bowdich, 1822. Stewart (1927:330) mistakenly list-

ed this name as being published in February 1822, on page xxiv [*sic*] of Férussac, and chose Bowdich's name as having priority. However, page xxxiv of Férussac was not published until April 13, 1822 (Kennard, 1942a:106).

AMPULLINA "Lamarck" Deshayes, 1830:36. *Nomen nudum;* see *Ampullina* Bowdich, 1822.

AMPULLINE "Lamarck" Defrance, 1821:446. Used in the vernacular; *nomen nudum*. See *Ampullina* Bowdich, 1822.

AMPULLINOPSIS Conrad, 1865:27. Type species *Natica mississippiensis* Conrad, 1847; monotypy. Tertiary, S.E. United States. *Megatylotus* Fischer, 1885 is a synonym *fide* Wenz (1941:1020), the type species may also be synonyms. *Hahazimania* Yabe and Hatai, 1939 is probably also a synonym (MacNeil, 1984:96–97).

AMPULLONATICA Sacco, 1890b:40. Type species *Ampullaria ambulacrum* Sowerby, 1822; subsequent designation Cossmann, 1893:740. Tertiary, Europe. Also listed in Sacco, 1890a:208 (315), but with a nude name as the sole species [*Ampullonatica repressa* "Rov."; species later validated by Sacco (1890b:40)]. Proposed as a subgenus of *Sigaretus* Lamarck, 1799 [=*Sinum* Röding, 1798]. Herein treated as a junior subjective synonym of *Euspira* Agassiz in Sowerby, 1837.

AMPULLOOSPIRA "Harris" Akopyan, 1976:245. Error for *Ampullospira* Harris, 1897.

AMPULLOPSIS Repelin, 1902. Type species *Ampullaria faujasi* "de Serres, 1875" [=*Ampullaria faujasii* Bronn, 1848; based on figures in Faujas, 1809]; monotypy. Upper Cretaceous, France. The illustrations are of an indeterminate shell with very tabulate whorls and an oddly compressed aperture that might belong to the Ampullospirinae. However, it is herein treated as *nomen dubium*.

AMPULLOSPIRA Harris, 1897:265. Type species *Euspira canaliculata* Morris and Lycett, 1854; original designation. Tertiary, Europe. Proposed as a subgenus of *Euspira* Agassiz in Sowerby, 1837 for the *Euspira sensu* Cossmann (1888:173). Harris (1897:266) also referred *Ampullina* (*Euspira*) *effusa* Tate, 1893 to *Ampullospira;* however, Tate's species is non-naticid, with a high spire, a flaring outer lip, and an everted columellar lip. Wenz (1941: 1020) erroneously listed *Ampullospira* as a synonym of *Pseudamaura* Fischer, 1885 (*q.v.*). *Ampulospira* Hanna, 1927 and *Ampulloospira* Akopyan, 1976, errors.

AMPULOSPIRA Hanna, 1927:306. Error for *Ampullospira* Harris, 1897.

ANOMPHALA "Jonas" Herrmannsen, 1846:61. Type species *Natica fluctuata* G. B. Sowerby, 1825; original designation. Recent, Indo-Pacific. Is a junior objective synonym of *Cernina* Gray, 1842. Compare *Globularia* Swainson, 1840.

AUSTROCOCHLIS Finlay and Marwick, 1937:51. Type species *Natica substolida* Tate, 1893; original designation. Oligocene, Australia.

BANIS Stephenson, 1941:279. Type species *Banis siniformis* Stephenson, 1941; original designation. Upper Cretaceous, Texas, U.S.A. Of uncertain status; possibly a synonym of *Gyrodes* Conrad, 1860 (*q.v.*).

BENSONIA Gray, 1847:150; *ex* Cantor MS. Published in synonymy of *Laguncula* Benson, 1842. *Bensonia* Pfieffer, 1855 was renamed *Bensonies* Baker, 1938 (Pulmonata: Ariophantidae) and *Bensonia* Malaise, 1935 was renamed *Bensoniana* Malaise, 1942 (Hymenoptera). See *Euspira* Agassiz in J. Sowerby, 1837.

BILLIEMIA Gregorio, 1930:14. Type species *Natica diblasii* Gemmellaro, 1869; original designation. Triassic, Italy. Proposed as a subgenus of *Natica* Scopoli, 1777. Herein rejected as a *nomen dubium* as the illustrations are indeterminate.

BOREONATICA Golikov and Kusakin, 1974:294. Type species *Natica clausa* Broderip and Sowerby, 1829; original designation. Recent, circumboreal. A junior subjective synonym of *Cryptonatica* Dall, 1892 (*fide* Golikov and Kusakin, 1978:153, who thought that *clausa* was the type species of *Cryptonatica*).

BULBOSOIDES Pan, 1982:101, 109. Type species *Bulbosoides glomus* Pan, 1982; original designation. Jurassic, China. Proposed as a subgenus of *Bulbus* Brown in Smith, 1839.

BULBUS Brown in Smith, 1839:94, 103. Type species *Bulbus smithii* Brown in Smith, 1839; monotypy [=*Natica fragilis* Leach, 1819]. Recent, North Atlantic. *Acrybia* H. and A. Adams, 1853 is a synonym. *Non Bulbus* "Humphr." Herrmannsen, 1846: 135 (*ibid.*, 1847:388, 1852:20, 117) = *Rapa* Röding, 1798 (Coralliophilidae). See Dell (1990:153–159) for further discussion of the possible relationships of this genus and the Antarctic species referable to *Bulbus*.

CALINATICINA Burch and Campbell, 1963:221. Type species *Sigaretus oldroydii* Dall, 1897; original designation. Recent, eastern Pacific.

CARINACCA Marwick, 1924:553. Type species *Ampullina waihaoensis* Suter, 1917; original designation. Eocene, New Zealand.

CATINUS Blainville, 1827:105; of "Lamarck, Klein and Martini." *Nomen nudum*. *Non Catinus* Fabricius, 1823 (rejected work; name referable to the Velutinidae). See also *Catinus* Oken, 1835 and *Catinus* H. and A. Adams, 1853. Is a junior subjective synonym of *Sinum* Röding, 1798.

CATINUS Oken, 1835:538. *Nomen nudum; non* Fabricius, 1823. Is a junior subjective synonym of

Sinum Röding, 1798. See also *Catinus* H. and A. Adams, 1853.

CATINUS H. and A. Adams, 1853:212; *ex* Klein, *non* Fabricius, 1823. Type species not designated: 25 species listed, all referable to *Sinum*. Is a junior subjective synonym of *Sinum* Röding, 1798.

CEPATIA Gray, 1840:151. In list; *nomen nudum*. See *Cepatia* Gray, 1842.

CEPATIA Gray, 1842:60. Type species *Natica cepacea* Lamarck, 1804; subsequent designation Gray, 1847:149. Eocene, Europe. *Velainia* Munier-Chalmas, 1884 and *Pseudocepatia* Magne and Vergneau-Saubade, 1973 are synonyms, and *Pitonillus* Férussac, 1822 is an error and is not a senior synonym.

CERNINA Gray, 1840:151. In list; *nomen nudum*. See *Cernina* Gray, 1842.

CERNINA Gray, 1842:60. Type species *Natica fluctuata* G. B. Sowerby, 1825; subsequent designation Gray, 1847:150. Recent, Indo-Pacific. Is not naticid; Kase (1990:565) transferred the type species to the Architaenioglossa, of unknown superfamilial placement. However, Kase erroneously used "*Globularia*" for *Natica fluctuata* and was unjustified in concluding that the entire Ampullospirinae was to be removed from the Naticidae. *Anomphala* Herrmannsen, 1846 is a junior objective synonym. *Cervina* Gray, 1857 is a misspelling. Compare with *Globularia* Swainson, 1840.

CERVINA Gray, 1857: vii, 50. Error for *Cernina* Gray, 1842.

CHILOCYCLUS Bronn in Bronn and Roemer, 1851: 75. Type species *Cochlearia carinata* Münster, 1841; monotypy. Triassic, Europe. No family originally indicated; Diener (1926:127) placed this in the Naticidae; Wenz (1940:752) transferred this to the Diastomidae. *Non Chilocyclus* Gill, 1863 (Gastropoda: Pomatiopsidae).

CHORISTES Carpenter in Dawson, 1872:392. Type species *Choristes elegans* Carpenter in Dawson, 1872; monotypy. Pleistocene, eastern Canada. Has often been placed in the Rissoacea as a separate family Choristidae (*e.g.*, Thiele, 1929:179 and Wenz, 1941:649–650). However, Golikov and Starobogatov (1975:212, 220) and Marincovich (1977:338) transferred this genus to the Naticidae. This confusion was clarified by Kabat (1989), especially with regard to the family name Choristidae.

CIGARETUS Hall, 1859:98. Error for *Sigaretus* Lamarck, 1799.

COCHLIS Röding, 1798:146. Type species *Cochlis flammea* Röding, 1798 [=*Natica vittata* (Gmelin, 1791)]; subsequent designation Hedley, 1916:51. Recent, eastern Atlantic. The later designation of *Cochlis albula* Röding, 1798 [=*Natica vitellus* (Linnaeus, 1758)] as type species, by Iredale (1924:254), resulted in the erroneous conclusion (*e.g.*, Cernohorsky, 1971:173) that *Cochlis* was a junior subjective synonym of *Natica* Scopoli, 1777. However, the earlier, overlooked designation of Hedley established *Cochlis* as a distinct genus (Oyama, 1985: 20).

CONUBER Finlay and Marwick, 1937:53. Type species *Natica conica* Lamarck, 1822; original designation. Recent, Australia. Proposed as a subgenus of *Polinices* Montfort, 1810.

CORONATICA Blanckenhorn, 1927:134. Type species *Neritopsis ornata* Fraas, 1878; subsequent designation Wenz, 1941:530. Cretaceous, Syria. Probably not naticid: Wenz placed this in the Purpurinidae.

CROMMIUM Cossmann, 1888:173 [177]. Type species *Ampullaria willemeti* Deshayes, 1825; original designation. Eocene, Europe. Palmer (1937:135) listed *Lupia* Conrad, 1865 as a synonym of *Crommium*.

CRYOTONATICA Oyama, 1969:70. Error for *Cryptonatica* Dall, 1892.

CRYPTONATICA Dall, 1892:362. Type species *Natica* (*Cryptonatica*) *floridana* Dall, 1892; subsequent designation Cossmann, 1896:238. Tertiary, S.E. United States. Proposed as a subgenus of *Natica* Scopoli, 1777. The designation of *Natica clausa* Broderip and Sowerby, 1829 as the type species came later and is not available (Dall, 1909:85; see Petit, 1986:38). *Boreonatica* and *Sulconatica* both of Golikov and Kusakin, 1974 are synonyms. *Crytonatica* Dall, 1921; *Cryptonica* Cossmann, 1925 and *Cryotonatica* Oyama, 1969 are errors. *Cryptonatica* Cossmann (1925:184, 301) is an error for *Cryptonerita* Kittl, 1894.

CRYPTONICA Cossmann, 1925:121. Error for *Cryptonatica* Dall, 1892.

CRYPTOSTOMUS Blainville, 1818a:120. Type species not designated; two species listed in original: *C. leachii* and *C. breviculus*, both of Blainville, 1818. Is a junior subjective synonym of *Sinum* Röding, 1798. *Cryptostoma* Blainville (1818b:126) is a variant spelling. Wenz (1941:1038) incorrectly attributed *Cryptostomus* to Rang, 1829; however, Rang (1829:237) referred to Blainville.

CRYTONATICA Dall, 1921:163. Error for *Cryptonatica* Dall, 1892.

DALLITESTA Mansfield, 1930:124. Type species "*Neverita coensis* Dall, 1903" [=*Polinices (Dallitesta) coensis* Mansfield, 1930]; original designation. Miocene, Florida, U.S.A. Herein treated as junior subjective synonym of *Euspira* Agassiz in Sowerby, 1837.

DESHAYESIA Raulin, 1844:1. Type species *Deshayesia parisiensis* Raulin, 1844; monotypy. Eocene, Europe. The figure shows columellar teeth

and this genus is herein referred to the Neritoidea. However, Wenz (1941:1023) used *Deshayesia* as a subgenus of *Globularia* Swainson, 1840 and stated that it is the proper name for *Naticella* Grateloup, 1847 *non* Swainson, 1840. Beets (1948) provided further discussion and a comparison with *Pisulina* Nevill and Nevill, 1869 (Neritidae).

ECTOSINUM Iredale, 1931:216–217. Type species *Ectosinum pauloconvexum* Iredale, 1931; original designation. Recent, Australia. A junior subjective synonym of *Sinum* Röding, 1798.

ELACHISINA Dall, 1918:137. Type species *Elachisina grippi* Dall, 1918; monotypy. Recent, eastern Pacific. Although Wenz (1941:1028) considered this to be naticid, it is a rissoidean (Coan, 1964; Ponder, 1985b).

EOCERNINA Gardner and Bowles, 1934:243. Type species *Natica hannibali* Dickerson, 1914; original designation. Eocene, Oregon–California, U.S.A. Proposed as a subgenus of *Cernina* Gray, 1842. As a full genus, discussed by Marincovich (1977:228–231).

EUCARYORUM Ehrenberg, 1831:46. Type species *Nerita mammilla* Linnaeus, 1758; monotypy. Also spelled as *Eucaryum* by the author. A junior subjective synonym of *Polinices* Montfort, 1810.

EUNATICA Melvill, 1899:92. Species mentioned: *Natica ponsonbyi* Melvill, 1899 and *Natica spadicea* (Gmelin, 1791) [=*Natica vitellus* (Linnaeus, 1758)]. *Natica spadicea* is herein designated as the type species, thus rendering *Eunatica* a junior objective synonym of *Natica* Scopoli, 1777.

EUNATICA Habe and Ito, 1965:30 (also in Okutani, 1968:29–30). Error for *Euspira* Agassiz in J. Sowerby, 1837 (not used in the context of *Eunaticina* Fischer, 1885). A junior homonym but not a synonym of *Eunatica* Melvill, 1899.

EUNATICINA Fischer, 1885:768. Type species *Nerita papilla* Gmelin, 1791; monotypy (of *Naticina* Gray, 1847). Recent, Indo-Pacific. A replacement name for *Naticina* Gray, 1847 *non* Guilding, 1834. *Sigaretotrema* Sacco, 1890, *Propesinum* Iredale, 1924, and *Pervisinum* Iredale, 1931 are all junior subjective synonyms.

EUSPIRA Agassiz in J. Sowerby, 1837a,b:14. Type species *Natica glaucinoides* J. Sowerby, 1812 (*non* Deshayes, 1832) [? = *Natica labellata* Lamarck, 1804]; subsequent designation Bucquoy, Dautzenberg, and Dollfus, 1883:143. Eocene, Europe. Cox (1930:168) stated that *glaucinoides* was a synonym of *labellata*, whereas Wrigley (1949:16) maintained that they were separate species. The designation of *Ampullaria sigaretina* Lamarck, 1804 (Gabb, 1877: 278 and Harris, 1897:265) is not valid, as that species was not listed under *Euspira* by Agassiz until 1842; however, *sigaretina* is the type of *Globularia* (*q.v.*). Similarly, Cossmann (1888:173) listed the type as *Euspira canaliculata* Morris and Lycett, 1854, but this taxon is obviously not available, either. See *Ampullospira* Harris, 1897 for the *Euspira sensu* Cossmann. Synonyms include *Laguncula* Benson, 1842, *Bensonia* Gray, 1847, *Lunatia* Gray, 1847 (as determined by Stoliczka, 1868:296), *Ampullonatica* Sacco, 1890, *Labellinacca* Cossmann, 1918 (based on *labellata* Lamarck), *Dallitesta* Mansfield, 1930, *Scarlatia* Schileyko, 1977, and *Pseudopolinices* Golikov and Sirenko, 1983. *Eunatica* Habe and Ito, 1965 is an error. *Euspira* was proposed for some of the same species that were listed under *Globulus* J. de C. Sowerby, 1835. Apparently Agassiz was unaware of that name for the fossil marine species formerly referred (by J. Sowerby) to *Ampullaria* Lamarck, 1799 (freshwater gastropod). Compare with *Globularia* Swainson, 1840. The species listed in 1837 for *Euspira* were *glaucinoides* and *depressa;* the species listed in 1842 were *acuta*, *patula*, *sigaretina*, *ambulacrum*, *conicus*, *rotundatus*, and *nobilis*. See Cleevely (1974:452–453) on Agassiz's French and German translations of Sowerby's *Mineral Conchology*. Melvill (1897:470) attributed *Euspira* to "Desor and Agassiz, 1837"; however, Desor was merely the translator while Agassiz was the author of the footnote containing this new name.

EUSPIROCROMMIUM Sacco, 1890a:208 (315). Type species *Natica elongata* Michelotti, 1861 *non* Hoeninghaus, 1829 [=*Crommium (Euspirocrommium) degensis* Sacco, 1890b]; monotypy. Tertiary, Europe. As a subgenus of *Crommium* Cossmann, 1888, by Sacco (1890b:41–42). Cox (1930: 173–174) attempted to clarify Cossmann's (1893: 741) confusion with respect to this taxon; however, Cox's conclusions were based on a single specimen which is not confamilial with the type species. Herein referred to the Phasianellidae (Archaeogastropoda).

FALSILUNATIA Powell, 1951:119. Type species *Natica soluta* Gould, 1848; original designation. Recent, sub-Antarctic. Dell (1990:145–153) redescribed the genus and reviewed its numerous antiboreal species.

FORATOR Taylor, Cleevely, and Morris, 1983:524, 526 [figure 2A], 553. One species mentioned "*Forator parkinsoni* Morris and Cleevely." Cretaceous, England. Genus and species are *nomina nuda*.

FRIGIDILACUNA Tomlin, 1930:23. Replacement name for *Sublacuna* Thiele, 1912 *non* Cossmann, 1899. Is a junior objective synonym of *Prolacuna* Thiele, 1913 (*q.v.*).

FRIGINATICA Hedley, 1916:51. Type species *Natica beddomei* Johnston, 1884; original designation [=*N. effosa* Watson, 1886; =(?)*N. polita* Tenison-Woods, 1875]. Recent, S. Australia. *Sulconacca* Marwick, 1924 is a junior subjective synonym.

FROVINA Thiele, 1912:196–197. Type species *Frovina soror* Thiele, 1912; monotypy. Recent, Antarctica.

GENNAEOSINUM Iredale, 1929:279–280. Type species *Gennaeosinum peleum* Iredale, 1929; original designation. Recent, Australia. The type species and several other congeneric Indo-Pacific species were illustrated and redescribed by Kilburn (1988) and Loch (1988). Herein treated as a junior subjective synonym of *Sigatica* Meyer and Aldrich, 1886.

GLAUSOLOX Maeda, 1988:123. Error for *Glossaulax* Pilsbry, 1929.

GLAUSSOLAX Maeda, 1988:123. Error for *Glossaulax* Pilsbry, 1929.

GLOBISINUM Marwick, 1924:573. Type species *Sigaretus drewi* Murdoch, 1899; original designation. Cenozoic, New Zealand. Dell (1956:42–46) provided extensive discussion of this genus and its potential relationships with *Acrybia* [=*Bulbus*]. *Globisium* Zinsmeister and Camacho, 1982:302, error.

GLOBISIUM Zinsmeister and Camacho, 1982:302. Error for *Globisinum* Marwick, 1924.

GLOBULARIA Swainson, 1840:345. Type species *Ampullaria sigaretina* Lamarck, 1804; subsequent designation Herrmannsen, 1847 [April 18]: 480. Eocene, Europe. *Globularia* was a replacement name for *Globulus* J. de C. Sowerby, 1835, *non* Schumacher 1817 (Trochidae). The designation (Gray, 1847 [post Nov. 9]:150) of *Natica fluctuata* G. B. Sowerby, 1825 (as the type species) not only came later but also is invalid as it was not an originally included species; see *Cernina* Gray, 1842. Compare with *Euspira* Agassiz in J. Sowerby, 1837. *Gobularia* Stewart, 1927 is a misspelling. Kase (1990: 565) erroneously placed *Natica fluctuata* (which he proved was not a naticid) in *Globularia*.

GLOBULUS J. de C. Sowerby, 1835:246; *non* Schumacher, 1817 (Trochidae). No type species designated; see the discussion under *Euspira* Agassiz in J. Sowerby, 1837 and *Globularia* Swainson, 1840. *Globulus* was a new generic name for the marine species formerly referred to *Ampullaria* Lamarck, 1799 (a freshwater gastropod genus). The species listed for *Globulus* were *depressus*, *acuta*, *patula*, *sigaretina*, *ambulacrum*, *nobilis*, and *helicoides*.

GLOSSAULAX Pilsbry, 1929:113. Type species *Natica reclusiana* Deshayes, 1839; original designation. Recent, eastern Pacific. *Golossaulax* Oyama, 1969; *Grossaulax* Oliveira, Rezende, and de Castro, 1981; *Glausolox* and *Glaussolax*, both Maeda, 1988, errors.

GLYPHEPITHEMA Rehder, 1943:196. Type species *Natica idiopoma* Pilsbry and Lowe, 1932; original designation. Recent, eastern Pacific.

GLYPTANATICA Gardner, 1947:555–556. Type species *Sigatica euglypta* Gardner, 1947; original designation. Tertiary, Florida, U.S.A. Proposed as a subgenus of *Sigatica* Meyer and Aldrich, 1886. Herein treated as a junior subjective synonym of *Sigatica* Meyer and Aldrich, 1886.

GOBULARIA Stewart, 1927:330. Error for *Globularia* Swainson, 1840.

GOLOSSAULAX Oyama, 1969:70. Error for *Glossaulax* Pilsbry, 1929.

GREGGSIA Cossmann, 1925:13, 47. Type species *Natica alabamiensis* Whitfield, 1865; original designation. Eocene, S.E. United States. Proposed as a subgenus of *Crommium* Cossmann, 1888. Is a junior objective synonym of *Lacunaria* Conrad, 1866.

GROSSAULAX Oliveira, Rezende, and de Castro, 1981:125. Error for *Glossaulax* Pilsbry, 1929.

GYRODES Conrad, 1860:289. Type species *Natica (Gyrodes) crenata* Conrad, 1860 (*non Natica crenata* Zekeli, 1852 *nec* Récluz, 1853); subsequent designation Gardner, 1916:496. The subsequent designation of Meek (1876:309) is not valid as Meek listed *crenata* as an "example" (*contra* Stewart, 1927:329). According to Stephenson (1923:357, 1941: 279) and Gardner (1945:169), the type species is a junior synonym of *Rapa supraplicata* Conrad, 1858. Cretaceous, S.E. United States. Proposed as a subgenus of *Natica* Scopoli, 1777. Compare with *Banis* Stephenson, 1941 and *Sohlella* Popenoe, Saul, and Susuki, 1987.

GYRODISCA Dall, 1896:44. Type species *Fossarus depressus* Seguenza, 1874; original designation [Dall cited this as "*Adeorbis depressus* Jeffreys"]. Cenozoic, Europe. Proposed as a subgenus of *Gyrodes* Conrad, 1860. Is not naticid. Dall (1903:1633) synonymized this with *Macromphalina* Cossmann, 1888; Warén and Bouchet (1988:85) synonymized *Gyrodisca* with *Megalomphalus* Brusina, 1871 (Vanikoridae).

HAHAZIMANIA Yabe and Hatai, 1939:209. Type species *Hahazimania hahazimensis* Yabe and Hatai, 1939; original designation. Tertiary, Japan. A junior subjective synonym of *Ampullinopsis* Conrad, 1865 *fide* MacNeil (1984:97).

HALIOTINELLA Souverbie in Souverbie and Montrouzier, 1875:33. Type, *Haliotinella montrouzieri* Souverbie, 1875; monotypy. Recent, Indo-Pacific.

HELICONATICA Dall, 1924:90. Type species *Eunaticina* (*Heliconatica*) *margaritaeformis* Dall, 1924; original designation. Recent, Hawaii. Proposed as a subgenus of *Eunaticina* Fischer, 1885. Herein treated as a junior subjective synonym of *Sigatica* Meyer and Aldrich, 1886.

HELIGMOPE Tate, 1893:328–329. Type species *Heligmope dennanti* Tate, 1893; monotypy. Tertiary, Australia. Is not naticid, possibly is a juvenile Trochoidea, although Wenz (1941:1036–1037) placed this as a subgenus of *Bulbus* Brown in Smith, 1839.

HELIX Linnaeus, 1758:768. Type species *Helix pomatia* Linnaeus, 1758; subsequent designation Montfort, 1810:231. Recent, Europe. A genus of land snails which was used for a number of pre-1850 naticid species. *Non Helix* Férussac, 1821:23.

HYPTERITA Woodring, 1957:92. Type species *Natica helicoides* Gray, 1825; original designation. Recent, eastern Pacific. Proposed as a subgenus of *Neverita* Risso, 1826.

ISONEMA Meek and Worthen, 1865:251–252. Type species *Isonema depressum* Meek and Worthen, 1865; monotypy. Proposed as a subgenus of *Holopea* Hall, 1847. Devonian, Ohio, U.S.A. Tryon (1886:8) placed this in the Naticidae but it is now referred to the Anomphalidae (Archaeogastropoda) (Knight, 1941:160–161; Knight, Batten, and Yochelson, 1960:I244, fig. 156.6).

KERGUELENATICA Powell, 1951:117. Type species *Natica grisea* Martens, 1878 (*non* Requien, 1848); original designation. Recent, sub-Antarctic. Proposed as a subgenus of *Amauropsis* Morch, 1857. As the type species is a junior homonym, it was renamed *Kerguelenatica bioperculata* Dell, 1990 (pp. 144–145).

KITTLIA Cossmann, 1909:8. Replacement name for *Ptychostoma* Laube, 1866; *non Ptychostomus* Agassiz, 1855 (Pisces). Triassic, Europe. Wenz (1939: 527) referred this to the Purpurinidae.

LABELLINACCA Cossmann in Cossmann and Peyrot, 1918:188. Type species *Natica labellata* Lamarck, 1804; monotypy. Tertiary, Europe. See also Cossmann, 1919:193. Is a junior objective synonym of *Euspira* Agassiz in Sowerby, 1837.

LACUNARIA Conrad, 1866:77. Type species *Natica alabamiensis* Whitfield, 1865; subsequent designation Cossmann, 1888:127. Eocene, S.E. United States. Tryon (1886:10) erroneously placed this genus in the Lacunidae. *Greggsia* Cossmann, 1925 is a junior objective synonym. *Lacunella* Dall, 1884 *non* Deshayes, 1864 was renamed *Lacunaria* Dall, 1885 *non* Conrad, 1866 and renamed again *Haloconcha* Dall, 1886 (Littorinidae).

LAGUNCULA Benson, 1842:488. Type species *Laguncula pulchella* Benson, 1842: monotypy. Recent, China ("said to inhabit canals"). Original description did not indicate familial placement. Gray (1847:150) and Philippi (1853:182) referred this to the Naticidae. Pease (1869:164) placed this in the Assimineidae. Thiele (1929:115) and Wenz (1941: 495) provisionally assigned this to the Viviparidae. Yen (1942:211, pl. 16, fig. 95) illustrated the type specimen and transferred this back to the Naticidae. The species appears to be a senior synonym of *Natica gilva* Philippi, 1842 [=*Natica fortunei* Reeve, 1855], which is now referred to *Euspira* [=*Lunatia*]. Herein treated as a junior subjective synonym of *Euspira* Agassiz in J. Sowerby, 1837. *Bensonia* Gray, 1847, *Lunatia* Gray, 1847, and *Scarlatia* Schileyko, 1977 are equivalent to *Laguncula*.

LOBOSTOMA Cossmann, 1885:147, *non* Berthold in Latreille, 1827 (Cestoidea); *nec* Rafinesque, 1831 (fossil Anthozoa); *nec* Gundlach, 1840 (Chiroptera); *nec* Amyot and Serville, 1843 (Hemiptera); *nec* Fairmaire, 1892 (Coleoptera). Type species not designated (eight species included); see *Naricopsina* Chelot, 1886.

LUNAIA Berry, 1964:148. Type species *Lunaia lunaris* Berry, 1964; original designation. Recent, eastern Pacific.

LUNATIA Gray, 1847:149. Type species *Natica ampullaria* Lamarck, 1822; original designation. Tertiary, Europe. *Lunatica* Tiba, 1985 *non* Röding, 1798 (Trochidae) is a *lapsus calami*. *Lunatia* is a junior subjective synonym of *Euspira*, as noted by Stoliczka (1868:296), Dall (1908:334, 1909:87) and Marincovich (1977:264). See also *Laguncula* Benson, 1842.

LUNATICA Tiba, 1985:19, *non* Röding, 1798 (Trochidae). Error for *Lunatia* Gray, 1847; corrected by Tiba, 1986:79.

LUPIA Conrad, 1865:27, *non* Robineau-Desvoidy, 1863 (Diptera). Type species *Ampullaria perovata* Conrad, 1846; monotypy. Tertiary, S.E. United States. Palmer (1937:135) placed this as a synonym of *Crommium* Cossmann, 1888, while Wenz (1941: 1026) considered this a synonym of *Amaurellina* Fischer, 1885.

MAGNATICA Marwick, 1924:553. Type species *Polinices planispirus* Suter, 1917 *non* Philipps, 1836 [renamed *Natica suteri* Marwick, 1924]; original designation. Tertiary, New Zealand.

MAMILLA Fabricius, 1823:98, 99. Type species not indicated; 23 species listed. No description provided. This work was rejected by the ICZN [Opinion 521, 1958]; hence, *Mamilla* is not available although the species included were naticids (see Herrmannsen, 1852:80). *Non Mamilla* Menke, 1830 (*q.v.*), *nec Mamilla* Wagner, 1907 (renamed *Weinlandella* Baker, 1954 [Gastropoda: Helicinidae]), *nec Mamilla* Scott, 1974 (renamed *Jascottella* Huddleston and Haman, 1982 [Foraminifera]).

MAMILLA "Schumacher" Menke, 1830:47. Error for *Mammilla* Schumacher, 1817. *Non Mamilla* Fabricius, 1823. This error was repeated by Agassiz (1848:644) and Wenz (1941:1030), *inter alia*.

MAMILLARIA Swainson, 1840:345. Type species *Mamillaria lactea* Swainson, 1840 [=*Nerita pesclephanti* Link, 1807]; subsequent designation Hedley, 1924:154. Recent, Indo-Pacific. Is a junior subjective synonym of *Neverita* Risso, 1826, *fide* Cernohorsky (1971:195) and Kilburn (1976:857); although Thiele (1929:261) and Wenz (1941:1028) listed this as a synonym of *Polinices* Montfort, 1810. *Mammillaria* (*e.g.*, Herrmannsen, 1847:17; Thiele,

192 261, 1931:761, and Wenz, 1941:1028, 1944: 1618) is a misspelling

MAMMA Blainville, 1823:475; *ex* Klein. *Nomen nudum*; compare with *Mamma* Mörch, 1852. Is a synonym of *Polinices* Montfort, 1810.

MAMMA Mörch, 1852:132; *ex* Klein. Published in synonymy of *Polinices* Montfort, 1810. Wenz (1941: 1030), in error, listed *Mamma* as a synonym of *Mammilla* Schumacher, 1817; however, Wenz was referring to Mörch's citation (also on page 132) of "*Mamma mulieris indicae* Chemnitz" (a name from an invalid work) under *Mammilla* Schumacher, 1817.

MAMMILLA Schumacher, 1817:58, 190. Type species *Mammilla fasciata* Schumacher, 1817; monotypy [=*Albula mammata* Röding, 1798]. Recent, Indo-Pacific. Synonyms include *Mamilla* Menke, 1830, *Naticaria* Swainson, 1840, *Ruma* Gray, 1847 and H. and A. Adams, 1853, and *Sigaretopsis* Cossmann, 1888.

MAMMILLARIA "Swainson" Herrmannsen, 1847: 17 (also, Thiele, 1929:261, 1931:761; and Wenz, 1941:1028, 1944:1618). Error for *Mamillaria* Swainson, 1840.

MEGATYLOTUS Fischer, 1885:766. Type species *Ampullaria crassatina* Lamarck, 1804; monotypy. Miocene, Europe. See also Cossmann, 1919:195–196. Is a junior subjective synonym of *Ampullinopsis* Conrad, 1865, *fide* Wenz (1941:1020); MacNeil (1984:97) suggested that the type species may be synonyms.

NACCA Risso, 1826:148. Type species *Nerita fulminea* Gmelin, 1791; subsequent designation Herrmannsen, 1847:89. Recent, S.E. Atlantic. Is a junior subjective synonym of *Natica* Scopoli, 1777.

NANGGULANIA Martin, 1914:174. Type species *Nanngulania puruensis* Martin, 1914; monotypy. Eocene, Java. Not naticid; possibly in the Neritoidea. Cossmann (1925:30–32) considered this to be a synonym of *Deshayesia* Raulin, 1844. *Nanggullania* Neave, 1940, error.

NANGGULLANIA Neave, 1940:261. Error for *Nanggulania* Martin, 1914.

NARICARIUS "Duméril, 1895" Macpherson and Gabriel, 1962:138. Error for *Naticarius* Duméril, 1806

NARICOPSINA Chelot, 1886:9. Replacement name for *Lobostoma* Cossmann, 1885 *non* Berthold in Latreille, 1827 (*et al.*). Type species *Neritopsis guerangeri* Cossmann, 1885; subsequent designation Chelot, 1886:9 Jurassic, Europe.

NATELLA Palmer, 1937:112, *non* Watson, 1934 (Pulmonata Paryphantidae). Type species *Natica magnoumbilicata* Lea, 1833; original designation. Eocene Alabama, U.S.A. Proposed as a section of *Natica (Naticarius)*. Renamed *Tella* Palmer, 1942 (*q.v.*).

NATICA Scopoli, 1777:392. Type species *Nerita vitellus* Linnaeus, 1758; subsequent designation Anton, 1838:31. Recent, Indo-Pacific. *Nerita canrena* Linnaeus, 1758 is not available as the type since it was not mentioned by Scopoli (*contra* Lamarck, 1799:77; Cossmann, 1888:159; Dall, 1892:362; *et al.*). Synonyms include *Ampullina* Férussac, 1822 *non* Bowdich, 1822, *Mamilla* Fabricius, 1823, *Nacca* Risso, 1826, *Payraudeautia* Bucquoy, Dautzenberg, and Dollfus, 1883.

NATICA Lamarck, 1799:77. Type species *Nerita canrena* Linnaeus, 1758; monotypy. A junior homonym but not a synonym of *Natica* Scopoli, 1777; is equivalent to *Naticarius* Duméril, 1806. Dodge (1947:67) differentiated between Scopoli's and Lamarck's use of Adanson's (pre-Linnaean) "Natica."

NATICA Risso, 1826:147. Type species never selected; three included species: *Nerita glaucina* Linnaeus, 1758 (a *nomen dubium*), *Natica marmorata*, and *N. pulchella*, both Risso, 1826 (referable to *Euspira*). A junior homonym but not a synonym of *Natica* Scopoli, 1777.

NATICARIA Swainson, 1840:346. Type species "*N. melanostoma* Martini" Swainson, 1840 [=*Nerita melanostoma* Gmelin, 1791]; subsequent designation Hedley, 1924:154. Recent, Indo-Pacific. Is a junior subjective synonym of *Mammilla* Schumacher, 1817.

NATICARINUS Noda, 1980:16. Error for *Naticarius* Duméril, 1806.

NATICARIUS Duméril, 1806:164. Type species *Nerita canrena* Linnaeus, 1758; subsequent designation Froriep, 1806:165. Recent, western Atlantic. *Naticus* Montfort 1810, *Quantonatica* Iredale, 1936, and *Tella* Palmer, 1942 are synonyms. *Naricarius* Macpherson and Gabriel, 1962 and *Naticarinus* Noda, 1980 are misspellings. See Iredale (1916) on Froriep's German edition of Duméril's work. Kabat (1990:12–14) further discussed the problems with this generic name.

NATICE Dall, 1892:371. Error for *Natica* Scopoli, 1777.

NATICELLA Swainson, 1840:345; *ex* Guilding MS. Type species "*N. aurantia* Martini" Swainson, 1840 [=*Albula aurantium* Röding, 1798]; monotypy. Recent, Indo-Pacific. Is a junior subjective synonym of *Polinices* Montfort, 1810.

NATICELLA Münster, 1841:100. Type species not indicated; 10 species originally included. Triassic, Austria. Illustrations show strongly sculptured shells, which are possibly referable to the Vanikoridae. *Non Naticella* Swainson, 1840, *nec* Grateloup, 1847.

NATICELLA Grateloup, 1847:caption to pl. V; *non* Swainson, 1840. Type species *Natica neritoides*

Grateloup, 1827; monotypy. Tertiary, Europe. The figure shows this species to have a toothed columellar lip; it is presumably a neritoidean. Wenz (1941:1023) stated that *Deshayesia* Raulin, 1844 is the proper name for this taxon, as a subgenus of *Globularia* (see also Beets, 1948). *Non Naticella* Swainson, 1840, *nec* Münster, 1841.

NATICELLINA Perner, 1911:208–209. Type species *Naticella suavis* Perner, 1907; monotypy. Silurian, Bohemia. A junior subjective synonym of *Naticonema* Perner, 1903 (Knight, Batten, and Yochelson, 1960:I240; Platyceratidae).

NATICINA Guilding, 1834:30. Type species, *Naticina lactea* Guilding, 1834; original designation. Recent, western Atlantic. Is a junior subjective synonym of *Polinices* Montfort, 1810. *Naticina* Gray, 1840 (*n.n.*), 1842 (*n.n.*), and 1847 was renamed *Eunaticina* Fischer, 1885.

NATICINA Gray, 1840:151. In list; *nomen nudum*. *Non Naticina* Guilding, 1834. See *Naticina* Gray, 1842 and 1847.

NATICINA Gray, 1842:90. In list; *nomen nudum*. *Non Naticina* Guilding, 1834. See *Naticina* Gray, 1847.

NATICINA Macgillivray, 1843:4, 51, 124. Proposed as a family name; based on *Natica* Scopoli, 1777 and equivalent to Naticidae Forbes, 1838. *Non Naticina* Guilding, 1834.

NATICINA Gray, 1847:150; *non* Guilding, 1834. Type species *Nerita papilla* Gmelin, 1791; monotypy. Recent, Indo-Pacific. See *Eunaticina* Fischer, 1885.

NATICITES Krueger, 1823:390. Type species not indicated; two species originally included: *Naticites canrenae* [*sic*] and *Naticites millepunctatus*. A genus-group name for "fossils," based on the genus *Natica*, and a junior homonym of *Natica* Scopoli, 1777 [*International Code of Zoological Nomenclature*, 1985, Articles 20 and 56(c)].

NATICODON Ryckholt, 1851:75. Type species "*Natica globosa* Hoeninghaus, 1830" [=*Naticodon globosum* Ryckholt, 1851] (see Knight, 1941:204); subsequent designation Konick, 1881:6. Carboniferous, Belgium. A junior subjective synonym of *Naticopsis* McCoy in Griffith, 1842 (Knight, Batten, and Yochelson, 1960:I276; Neritopsidae). See Rosenberg and Petit (1987:56) for further discussion.

NATICONEMA Perner, 1903:caption to pl. 54. Type species *Naticonema similare* Perner, 1903; monotypy. Silurian, Bohemia. Now referred to the Platyceratidae (Knight, Batten, and Yochelson, 1960:I240, fig. 153.1).

NATICOPSIS McCoy in Griffith, 1842:19. Type species *Natica ampliata* Griffith, 1836; subsequent designation Jankowlew (1899:115). Carboniferous, Ireland. Tryon (1886:8) placed this in the Naticidae, but it is now referred to the Neritopsidae (Archaeogastropoda) (Knight, Batten, and Yochelson, 1960:I276, fig. 181.7–8; Rosenberg and Petit, 1987: 57).

NATICUS Montfort, 1810:218. Type species *Nerita canrena* Linnaeus, 1758; original designation. Is a junior objective synonym of *Naticarius* Duméril, 1806.

NATINA Nomura, 1935:130; Oliveira and Oliveira, 1984:43. Error for *Natica* Scopoli, 1777.

NATIRIA Konick, 1881:5. Type species *Natica lirata* Philipps, 1836; monotypy. Carboniferous, Belgium. Tryon (1886:14) placed this in the Vanikoridae. Knight, Batten, and Yochelson (1960:I300, fig. 196.2) referred this to the Craspedostomatidae (Archaeogastropoda).

NEOCRITA Sowerby, 1883:75. Error for *Neverita* Risso, 1826.

NERINATICA Olsson, 1930:68. Type species *Natica (Nerinatica) paytensis* Olsson, 1930; original designation. Eocene, Peru. Proposed as a subgenus of *Natica* Scopoli, 1777. Herein treated as a junior subjective synonym of *Sigatica* Meyer and Aldrich, 1886.

NERITA Linnaeus, 1758:776. Type species *Nerita peloronta* Linnaeus, 1758; subsequent designation Montfort, 1810:347. Recent, Caribbean. *Non Nerita* Rafinesque, 1815. A genus of marine archaeogastropods used for a number of pre-1850 naticid species.

NERITOIDES Meuschen, 1779:85. Type species *Nerita vitellus* Linnaeus, 1758; subsequent designation Kadolsky, 1971:191, 193. A junior objective synonym of *Natica* Scopoli, 1777.

NEVERITA Risso, 1826:149. Type species *Neverita josephinia* Risso, 1826; monotypy. Recent, Mediterranean. *Mamillaria* Swainson, 1840 is a synonym, *fide* Cernohorsky (1971:195) and Kilburn (1976:857). *Poliniciella* Petuch, 1988 is also a synonym. *Neocrita* Sowerby, 1883 and *Nevertita* Matsui, 1985 are misspellings.

NEVERTITA Matsui, 1985:173. Error for *Neverita* Risso, 1826.

NOTOCHLIS "Powell" Cotton, 1959:368, 433, 446. Error for *Notocochlis* Powell, 1933.

NOTOCOCHLIS Powell, 1933:166. Type species *Cochlis migratoria* Powell, 1927 [=*Natica gualteriana* Récluz, 1844]; original designation. Recent, New Zealand. *Notochlis* Cotton, 1959 and *Notocochris* Oyama, 1969, errors. Compare with *Cochlis* Röding, 1798; see Oyama (1985:20).

NOTOCOCHRIS Oyama, 1969:87. Error for *Notocochlis* Powell, 1933.

NUX Barnard, 1960:439. Type species *Nux alabaster* Barnard, 1960; original designation. Recent, South

Africa. Barnard stated that the shell was "naticoid" but that this was a Rhachiglossan (=Muricoidea) of an undetermined family. However, Salisbury, Edwards, and Curds (1963:89) listed this in the Naticidae.

ORTHOSPIRA Kutassy, 1940:346. Type species *Euspira saginata* Böhm, 1895; original designation. Triassic, Europe. A replacement name for *Euspira sensu* Böhm, 1895 *non* Agassiz in Sowerby, 1837. Not treated by Wenz (1938–1944). Herein transferred to the Coelostylinidae.

PACHYCROMMIUM Woodring, 1928:391. Type species *Amaura guppyi* Gabb, 1873; original designation. Miocene, Dominican Republic. *Pseudocrommium* Clark, 1946 is a junior subjective synonym.

PAOSIA Böhm, 1895a:146. Type species *Natica fadaltensis* Böhm, 1895; original designation. Cretaceous, Europe. Is not naticid: Wenz (Errata, 1943: 1495) transferred this to *Trajanella* in the Pseudomelaniidae.

PAPATECTONATICA Oyama, 1969:87. Error for *Paratectonatica* Azuma, 1961.

PARATECTONATICA Azuma, 1961:202. Type species *Cochlis tigrina* Röding, 1798; original designation. Recent, Japan. Possibly congeneric with *Notocochlis* Powell, 1933?

PARVISINUM "Iredale" Salisbury, 1932:65. Error for *Pervisinum* Iredale, 1931.

PAYRADEAUTIA "Bucquoy, Dautzenberg, and Dollfus" Wenz, 1941:1045. Error for *Payraudeautia* Bucquoy, Dautzenberg, and Dollfus, 1883.

PAYRANDEAUTIA Oliveira, Rezende, and de Castro, 1981:125. Error for *Payraudeautia* Bucquoy, Dautzenberg, and Dollfus, 1883.

PAYRAUDAUTIA Dollfus, 1883:94. Error for *Payraudeautia* Bucquoy, Dautzenberg, and Dollfus, 1883.

PAYRAUDEAUTIA Bucquoy, Dautzenberg, and Dollfus, 1883:137, 149. Type species *Natica intricata* Donovan, 1804; original designation. Recent, Europe. *Payraudautia* Dollfus, 1883; *Payreaudautia* Simroth, 1907; *Payradeautia* Wenz, 1941; and *Payrandeautia* Oliveira, Rezende, and de Castro, 1981; errors. Is a junior subjective synonym of *Natica* Scopoli, 1777.

PAYREAUDAUTIA Simroth, 1907:1044. Error for *Payraudeautia* Bucquoy, Dautzenberg, and Dollfus, 1883

PERVISINUM Iredale, 1931:216–217. Type species *Pervisinum dingeldeii* Iredale, 1931; monotypy. Recent, Australia. Kilburn (1976:869) as a junior subjective synonym of *Eunaticina* Fischer, 1885. *Parvisinum* Salisbury, 1932 is a misspelling.

PICTAVIA Cossmann, 1925:13–14. Type species *Natica pictaviensis* d'Orbigny, 1850; original designation. Triassic–Jurassic, Europe. Not naticid, of uncertain familial placement.

PITONILLUS Férussac, 1822:xxxiv. Error for *Pitonnillus* Montfort, 1810 (=*Umbonium* Link, 1807 [Gastropoda: Trochidae]; *fide* Wenz [1938:321]). However, Férussac (1825:378) and Bronn (1848: 781, 983), with reference to *Natica cepacea* Lamarck, 1804, erroneously placed this genus in the Naticidae. This error does not represent a "type species" and is of no consequence with respect to the validity of *Cepatia* Gray, 1842.

PLICONACCA Cossmann and Martin, in Martin, 1914:171. Type species *Natica (Pliconacca) trisulcata* Martin, 1914; monotypy. Eocene, Java. See Majima (1989:63) for comparison with *Glossaulax* Pilsbry, 1929.

POILYNICES Golikov, Gulbin, and Sirenko, 1987: 41. Error for *Polinices* Montfort, 1810.

POLINELLA Marwick, 1931:99. Type species *Uber obstructus* Marwick, 1924; original designation. Miocene, New Zealand. Proposed as a subgenus of *Polinices* Montfort, 1810.

POLINIA Desmarest, 1858:162. Error for *Polinices* Montfort, 1810.

POLINCIES Boss, Rosewater, and Ruhoff, 1968:241. Error for *Polinices* Montfort, 1810.

POLINICE Rang, 1829:190, 191. Error for *Polinices* Montfort, 1810.

POLINICES Montfort, 1810:222. Type species *Polinices albus* Montfort, 1810; original designation (=*Nerita mammilla* Linnaeus, 1758; frequently misspelled *mamilla* [*e.g.*, Cernohorsky, 1971:191, 193]). Recent, Indo-Pacific. The nomenclatural problems with the type species and this genus were clarified by Kabat (1990:16–18). Synonyms include *Albula* Röding, 1798, *Mamma* Blainville, 1823, *Eucaryorum* Ehrenberg, 1831, *Naticina* Guilding, 1834, *Naticella* Swainson, 1840, *Uber* Gray, 1847, and *Mamma* Mörch, 1852. Incorrect spellings include *Polinicis* Blainville, 1826, *Polinice* Rang, 1829, *Polynices* Menke, 1830, *Pollinices* Mörch, 1852, *Polinia* Desmarest, 1858, *Polinus* Hall, 1868, *Polincies* Boss, Rosewater, and Ruhoff, 1968, and *Poilynices* Golikov, Gulbin, and Sirenko, 1987.

POLINICIELLA Petuch, 1988:17. Type species *Poliniciella marylandica* Petuch, 1988; monotypy. Miocene, Maryland, U.S.A. Herein treated as a junior subjective synonym of *Neverita* Risso, 1826.

POLINICIS Blainville, 1826:310. Error for *Polinices* Montfort, 1810.

POLINUS Hall, 1868:46. Error for *Polinices* Montfort, 1810.

POLLINICES "Montfort" Mörch, 1852:132. Error for *Polinices* Montfort, 1810.

POLYNICES "Montfort" Menke, 1830:47. Error for *Polinices* Montfort, 1810. However, Herrmannsen

(1847:318) stated that this was a proper emendation for *Polinices* (*i.e.*, the masculine spelling).

PRAENATICA Perner, 1903:caption to pls. 55, 56 (also in Perner, 1907:caption to pl. 105, 1911:171–172). Type species *Strophostylus gregarius proeva* Perner, 1903; subsequent designation Knight (1941: 270). Silurian, Bohemia. Now placed in the Platyceratidae (Knight, Batten, and Yochelson, 1960:I240, fig. 153.8).

PRISCONATICA Gabb, 1877:277–278. Type species *Natica pedernalis* Roemer, 1849; original designation. Cretaceous, Texas, U.S.A. Of uncertain status, superficially similar to *Mammilla* Schumacher, 1817. Wenz (1941:1021) erroneously attributed *Prisconatica* to Pervinquiere, 1912 and listed it as a synonym of *Pseudamaura* Fischer, 1885.

PRISTINACCA Finlay and Marwick, 1937:51. Type species *Uber senisculus* Marwick, 1924; original designation. Paleocene, New Zealand.

PROBLITORA Iredale, 1931:216. Type species *Amauropsis moerchi* Adams and Angas, 1863; original designation. Recent, Australia. Placed in the Littorinidae by Iredale (1931). Rosewater (1970: 426) questionably referred this back to the Naticidae. It is now placed in the Epitoniidae (=*Alexania* Strand, 1928 *fide* Anders Warén, *in litt.*, Oct. 1989).

PROLACUNA Thiele, 1913:86. Type species *Sublacuna indecora* Thiele, 1912; monotypy (of *Sublacuna* Thiele, 1913). Recent, sub-Antarctic. Replacement name for *Sublacuna* Thiele, 1912 *non* Pilsbry, 1895. *Frigidilacuna* Tomlin, 1930 is a junior objective synonym. See Dell (1990:162–163) for a review of this genus.

PROPESINUM Iredale, 1924:183, 255. Type species *Natica umbilicata* Quoy and Gaimard, 1832; original designation. Recent, Australia. Herein treated as a junior subjective synonym of *Eunaticina* Fischer, 1885.

PROSIGARETUS Perner, 1907:caption to pl. 105 (also in Perner, 1911:210–211). Type species *Prosigaretus peronatus* Perner, 1907; monotypy. Silurian, Bohemia. A junior subjective synonym of *Praenatica* Perner, 1903 (Knight, Batten, and Yochelson, 1960:I240; Platyceratidae).

PROSTYLIFER Koken, 1889:446. Type species *Melania paludinaris* Münster, 1841; monotypy. Triassic, Europe. Is probably in the Melanopsidae, although Wenz (1941:1021) listed *Prostylifer* as a synonym of *Pseudamaura* Fischer, 1885 (*q.v.*).

PROXIUBER Powell, 1933:167. Type species *Lunatia australis* Hutton, 1878; original designation. Recent, New Zealand.

PSEUDAMAURA Fischer, 1885:767. Type species *Natica bulbiformis* Sowerby in Sedgwick and Murchison, 1832 (*nomen nudum*) (=*Natica bulbiformis* d'Orbigny, 1842 [pp. 162–163]; *ex* Sowerby); monotypy. Cretaceous, Europe. Wenz (1941:1021) listed as synonyms *Prostylifer* Koken, 1889, *Ampullospira* Harris, 1897, and *Prisconatica* "Pervinquiere, 1912." However, *Prostylifer* is probably in the Melanopsidae, *Ampullospira* is valid (Marincovich, 1977:231) and *Prisconatica* Gabb, 1877 is of uncertain status. Wolff and Schenk (1972) reviewed the type species and four other Cretaceous taxa referable to this genus.

PSEUDOCEPATIA Magne and Vergneau-Saubade, 1973:240. Type species *Natica crassiuscula* Grateloup, 1827; original designation. Tertiary, Europe. Proposed as a subgenus of *Cepatia* Gray, 1842. Herein treated as a junior subjective synonym of *Cepatia* Gray, 1842.

PSEUDOCROMMIUM Clark, 1946:18. Type species *Pseudocrommium carmenensis* Clark, 1946; original designation. Eocene, Colombia. Herein treated as a junior subjective synonym of *Pachycrommium* Woodring, 1928.

PSEUDOPOLINICES Golikov and Sirenko, 1983: 1339. Type species *Natica nana* Möller, 1842; original designation. Recent, circumboreal. Herein treated as a junior subjective synonym of *Euspira* Agassiz in Sowerby, 1837.

PSEUDOPOLYNICES Golikov, 1987:98. Error for *Pseudopolinices* Golikov and Sirenko, 1983.

PSEUDOTYLOSTOMA von Ihering, 1903:207. Type species *Pseudotylostoma romeroi* von Ihering, 1903; original designation. Cretaceous, Argentina. Herein rejected as a *nomen dubium*, based on an indeterminate specimen (Steinkern), although Wenz (1941:1021) listed this as subgenus of *Ampullina* Bowdich, 1822.

PSEUDOTYLOSTOMA Pchelintsev, 1963:38–39. Type species *Pterodonta corallinum* Étallon, 1859; original designation. Cretaceous, Europe. A junior homonym (but not a synonym) of *Pseudotylostoma* von Ihering, 1903. Pchelintsev placed von Ihering's name into the synonymy of *Tylostoma* Sharpe, 1848 and apparently he assumed that this action freed the name for subsequent reuse.

PTYCHOSTOMA Laube, 1866:45. Type species *Natica pleurotomoides* Wissmann in Münster, 1841; original designation. Triassic, Europe. *Non Ptychostomus* Agassiz, 1855 (Pisces): see *Kittlia* Cossmann, 1909. Wenz (1939:527) placed this in the Purpurinidae.

PUNCTOSPIRA Akopyan, 1976:27, 245. Type species *Tylostoma punctatum* Sharpe, 1849; original designation. Cretaceous, Europe. Compare with *Tylostoma* Sharpe, 1849.

QUANTONATICA Iredale, 1936:311. Type species *Natica subcostata* Tenison-Woods, 1878; original designation. Recent, Australia. Proposed as a subgenus of *Naticarius* Duméril, 1806. Herein treated as a junior subjective synonym of *Naticarius* Du-

méril, 1806; see Oyama (1985:20–21) for further discussion.

RAYNEVALLIA Ponzi, 1872:80. One species listed: *Raynevallia romulea* Ponzi, 1872 (*nomen nudum*). This taxon was subsequently validated as *Sigaretus raynevalli* Ponzi, 1876 (Cenozoic, Italy). Not an available name and is equivalent to *Sinum* Röding, 1798.

REUMA "Chemnitz" Récluz, 1851:197. Error for *Ruma* Gray, 1847.

RUMA Gray, 1847:149; *ex* Chemnitz. Type species *Natica maura* Lamarck, 1816; original designation. Recent, Indo-Pacific. Published in synonymy of *Mammilla* Schumacher, 1817.

RUMA H. and A. Adams, 1853:209; *ex* Chemnitz. Type species *Ruma mammillaris* "Born" (=indeterminate *Mammilla* species). A junior objective synonym of *Mammilla* Schumacher, 1817.

RUMELLA Bourguignat, 1885:89. Type species not indicated; two originally included species: *R. giraudi* Bourguignat, 1885 and *R. milne-edwardsiana* Bourguignat, 1885 (illustrated in Bourguignat, 1888: pl. 17; 4 additional species described in Bourguignat, 1890:250–258; all placed in the Naticidae). Freshwater, Lake Tanganyika. Not naticid and is referable to the Thiaridae (Cerithioidea). Vaught (1989:30) misspelled as "*Rumela*."

SCARLATIA Schileyko, 1977:80–81. Type species *Natica fortunei* Reeve, 1855; original designation. Recent, N.W. Pacific. Is a junior subjective synonym of *Laguncula* Benson, 1842; see *Euspira* Agassiz in J. Sowerby, 1837.

SEGARETUS Millar, 1817:332. Error for *Sigaretus* Lamarck, 1799.

SIGARETARIUS Duméril, 1806:164. Type species not indicated in original or by Froriep (1806:165; no example given); herein designated as *Helix haliotoidea* Linnaeus, 1758. Therefore *Sigaretarius* is a junior objective synonym of *Sinum* Röding, 1798. Compare with *Sigaretus* Lamarck, 1799.

SIGARETHUS Schinz in Cuvier, 1825:588. Error for *Sigaretus* Lamarck, 1799.

SIGARETIA Herrmannsen, 1852:123. Error for *Sigaretus* Lamarck, 1799.

SIGARETIGENUS Renier, 1807:tav. viii. Emendation of *Sigaretus* Lamarck, 1799. Renier's works were rejected by the ICZN [Opinion 427, 1956].

SIGARETOPSIS Cossmann, 1888:168 (172). Type species *Natica infundibulum* Watelet, 1853; original designation. Eocene, Europe. Herein treated as a junior subjective synonym of *Mammilla* Schumacher, 1817 (see also Cossmann, 1925:106–108).

SIGARETOTREMA Sacco, 1890a:207 (314). Type species *Sigaretus michaudi* Michelotti, 1847; monotypy. Tertiary, Europe. Subsequently treated as a subgenus of *Sigaretus* Lamarck, 1799 [=*Sinum* Röding, 1798] by Sacco (1890b:38). Herein treated as a junior subjective synonym of *Eunaticina* Fischer, 1885.

SIGARETUS Lamarck, 1799:77. Type species *Helix haliotoidea* Linnaeus, 1758; monotypy. Is a junior objective synonym of *Sinum* Röding, 1798. See also *Sigaretarius* Duméril, 1806 and *Sigaretigenus* Renier, 1807. *Segaretus* Millar, 1817, *Sigarethus* Schinz in Cuvier, 1825, *Sigeretus* Swainson, 1835, *Sigaretia* Herrmannsen, 1852, *Cigaretus* Hall, 1859, and *Siguretus* Martens, 1904 are misspellings.

SIGATICA Meyer and Aldrich, 1886:42 (106). Type species *Sigaretus (Sigatica) boettgeri* Meyer and Aldrich, 1886; monotypy. Tertiary, S.E. United States. Junior subjective synonyms herein include *Heliconatica* Dall, 1924, *Gennaeosinum* Iredale, 1929, *Nerinatica* Olsson, 1930, and *Glyptanatica* Gardner, 1947. *Sigaticus* Aldrich, 1887 is an unjustified emendation.

SIGATICUS Aldrich, 1887:83. An unjustified emendation for *Sigatica* Meyer and Aldrich, 1886.

SIGERETUS Swainson, 1835:7. Error for *Sigaretus* Lamarck, 1799.

SIGURETUS Martens, 1904:21. Error for *Sigaretus* Lamarck, 1799.

SINUBER Powell, 1951:120. Type species *Natica sculpta* Martens, 1878; original designation. Recent, sub-Antarctic. Dell (1990:160–162) reviewed the species referable to this genus.

SINUM Röding, 1798:14. Type species *Helix haliotoidea* Linnaeus, 1758; subsequent designation Dall, 1915:109. Recent, Indo-Pacific. Synonyms include *Sigaretus* Lamarck, 1799, *Sigaretarius* Duméril, 1806, *Cryptostomus* Blainville, 1818, *Catinus* H. and A. Adams, 1853, and *Ectosinum* Iredale, 1931. See also *Catinus* Blainville, 1827, *Catinus* Oken, 1835, and *Raynevallia* Ponzi, 1872. *Sisum* Oliveira, 1988; *Sinuni* and *Siunm*, both Oyama, 1969; errors. Kabat (1990:4–9) provided further discussion of this genus.

SINUNI Oyama, 1969:80. Error for *Sinum* Röding, 1798.

SISUM Oliveira, 1988:20. Error for *Sinum* Röding, 1798.

SIUNM Oyama, 1969:81. Error for *Sinum* Röding, 1798.

SOHLELLA Popenoe, Saul, and Susuki, 1987:78. Type species *Gyrodes canadensis* Whiteaves, 1903; original designation. Cretaceous, California, U.S.A.

SPELAENACCA Finlay, 1926:229. Type species *Magnatica altior* Finlay, 1926; original designation. Tertiary, New Zealand. Proposed as a subgenus of *Magnatica* Marwick, 1924.

STELZNERIA Geinitz, 1874:257. Type species *Stelz-*

neria cepacea Geinitz, 1874; monotypy. Cenozoic, Europe. Wenz (1941:1027) doubtfully placed *Stelzneria* as a subgenus of *Tylostoma* Sharpe, 1849. However, based on Geinitz's figure, *Stelzneria* is herein treated as an aberrant member of the Stiliferidae.

STIGMAULAX Mörch, 1852:133. Type species *Nerita sulcatus* Born, 1778; subsequent designation Harris 1897:262. Recent, western Atlantic. *Aloconatica* Shikama, 1971 is a synonym.

STOMATIA Gray, 1847:150; *ex* Hill (1752:119) and Browne (1756:398). *Non Stomatia* Helbling, 1779 (Trochoidea). Published in synonymy of *Sigaretus* Lamarck, 1799 [=*Sinum* Röding, 1798]. See *Stomatius* Herrmannsen, 1852.

STOMATIUS Herrmannsen, 1852:127; *ex* Hill (1752: caption to pl. 7). Gray (1847:150) and Tryon (1886: 10) both placed this in the synonymy of *Sigaretus*. The original descriptions referred to the Caribbean *Sinum maculatum* (Say, 1831). A junior subjective synonym of *Sinum* Röding, 1798.

SUBLACUNA Thiele, 1912:195–196, *non* Pilsbry, 1895, *nec* Cossmann, 1899. Type species *Sublacuna indecora* Thiele, 1912; monotypy. Recent, sub-Antarctic. Renamed *Prolacuna* Thiele, 1913 and *Frigidilacuna* Tomlin, 1930.

SULCONACCA Marwick, 1924:556. Type species *Sulconacca vaughani* Marwick, 1924; original designation. Tertiary, New Zealand. A synonym of *Friginatica* Hedley, 1916; *fide* Finlay and Marwick (1937:56).

SULCONATICA Golikov and Kusakin, 1974:294. Type species *Natica janthostoma* Deshayes, 1839; original designation. Recent, N.W. Pacific. Proposed as a subgenus of *Boreonatica* Golikov and Kusakin, 1974. Herein treated as a junior subjective synonym of *Cryptonatica* Dall, 1892.

TANEA Marwick, 1931:98. Type species *Natica zelandica* Quoy and Gaimard, 1832; original designation. Recent, New Zealand.

TANIELLA Finlay and Marwick, 1937:48. Type species *Natica notocenica* Finlay, 1924; original designation. Miocene, New Zealand. *Non Taniella* Kase, 1990 (Olividae).

TASMATICA Finlay and Marwick, 1937:51. Type species *Natica schoutanica* May, 1913; original designation. Recent, Tasmania.

TECTONATIC Maeda, 1988:124. Error for *Tectonatica* Sacco, 1890.

TECTONATICA Sacco, 1890b:33. Type species *Natica tectula* "Bors." Bonelli, 1826 (*nomen nudum*) [=*Natica (Tectonatica) tectula* Sacco, 1890b]; monotypy. Pliocene, Europe. Proposed as a subgenus of *Natica* Scopoli, 1777. Also listed in Sacco, 1890a:205 (312), but with a nude name as the sole species [*Tectonatica tectula* "Bon."]. *Cryptonatica* Dall, 1892 is not a synonym (*contra* Wenz, 1941: 1040, *inter alia*), see Marincovich (1977:405) and Oyama (1985:19). *Tectonica* Carcelles and Williamson, 1951; *Tectonatic* Maeda, 1988, errors.

TECTONICA Carcelles and Williamson, 1951:283. Error for *Tectonatica* Sacco, 1890.

TEJONIA Hanna and Hertlein, 1943:172. Type species *Natica alveata* Conrad, 1855 (*non* Troschel, 1852; = *Amaurellina moragai* Stewart, 1927); original designation. Eocene, California, U.S.A.

TELLA Palmer, 1924:674. Replacement name for *Natella* Palmer, 1937 (*q.v.*). Type species *Natica magnoumbilicata* Lea, 1833; original designation. Eocene, Alabama, U.S.A. Herein treated as a junior subjective synonym of *Naticarius* Duméril, 1806.

TRACHYDOMIA Meek and Worthen, 1866:364. Type species *Naticopsis nodosus* Meek and Worthen, 1860; original designation. Carboniferous, Illinois, U.S.A. Tryon (1886:8) placed this in the Naticidae. This taxon is currently referred to the Neritopsidae (Archaeogastropoda) (Knight, Batten, and Yochelson, 1960:I277, fig. 182.5).

TROCHONATICA Pchelintsev, 1963:34–35. Type species *Natica mexihoerensis* Choffat, 1886; original designation. Cretaceous, Europe. Superficially similar to *Globularia* or *Cernina;* herein rejected as a *nomen dubium*.

TURBO Linnaeus, 1758:761. Type species *Turbo petholatus* Linnaeus, 1758; subsequent designation Montfort, 1810:203. Recent, Indo-Pacific. A genus of marine archaeogastropods, this name was used for a number of pre-1850 naticid species (especially for fossils).

TYCHONIA Konick, 1881:7. Type species *Natica omaliana* Konick, 1843; monotypy. Carboniferous, Belgium. Tryon (1886:9) placed this in the Naticidae. Knight, Batten, and Yochelson (1960:I244, fig. 156.2) referred this to the Anomphalidae (Archaeogastropoda).

TYLOSTOMA Sharpe, 1849:378. Type species *Tylostoma torrubiae* Sharpe, 1849; subsequent designation White, 1880:142. The designation of *Tylostoma globosum* Sharpe, 1849 as type species by Wenz (1941:1026) came later. Cretaceous, Europe. Possibly referable to the Neritoidea? *Varigera* d'Orbigny, 1850 and *Varicigera* Douville, 1916 are junior synonyms. All three taxa have 2 varices on the shell and resemble extinct neritoideans. Tryon (1886:9–10) placed this genus in the Tornatellidae. Wenz (1941:1027) listed *Stelzneria* Geinitz, 1874 as a subgenus; however, that taxon is referable to the Stiliferidae. Numerous fossil species have subsequently been described for this genus and some may be naticid (*cf.* the descriptions in Mallada, 1887:57–59, pl. 18). A confused discussion of this taxon and its possible relationships with *Pterodonta* (Stromboidea: Colombellinidae) was provided by

Stoliczka (1867:35–41, 1868:292–294). Compare *Pseudotylostoma* von Ihering, 1903 and *Punctospira* Akopyan, 1976.

UBA "Humphreys" Fletcher, 1938:113. Error for *Uber;* only one species listed: *Uba fallai* Fletcher, 1938.

UBER Gray, 1847:149; *ex* Humphrey, 1797 (invalid work). Type species *Nerita mammilla* Linnaeus, 1758; subsequent designation Philippi, 1853:497. Recent, Indo-Pacific. Published in synonymy of *Polinices* Montfort, 1810. Also "described" by Dunker (1882:62) and by Cotton and Godfrey (1931:19).

UBERELLA Finlay, 1928:248. Type species *Natica vitrea* Hutton, 1873; original designation. Recent, New Zealand. Finlay compared this taxon with *Euspira*.

VANIKOROPSIS Meek, 1876:331. Type species *Natica tuomeyana* Meek and Hayden, 1856; original designation. Cretaceous, Nebraska, U.S.A. Is referable to the Vanikoridae on the basis of the shell sculpture (see Sohl, 1967:22).

VARICIGERA Douvillé, 1916:143. Unjustified emendation for *Varigera* d'Orbigny, 1850.

VARIGERA d'Orbigny, 1850:68, 103. Type species *Varigera rochatiana* d'Orbigny, 1850; subsequent designation Douvillé, 1916:144. Cretaceous, Europe. Is a junior subjective synonym of *Tylostoma* Sharpe, 1849 (see Stoliczka, 1868:293). *Varicigera* Douvillé, 1916 is an unjustified emendation.

VELAINIA Munier-Chalmas, 1884:335–336. Type species *Natica cepacea* Lamarck, 1804; original designation. Eocene, Europe. Is a junior objective synonym of *Cepatia* Gray, 1842.

VERNELIA Böhm, 1895b:250. Type species *Natica fastigiata* Stoppani, 1857; subsequent designation Woodward, 1896:76. Paleozoic, Europe. Now referred to the Neritopsidae (Archaeogastropoda) (Knight, Batten, and Yochelson, 1960:I276–1277, fig. 180A.2).

WALUIA Ladd, 1934:211. Type species *Globularia edwardsii* Ladd, 1934; original designation. Miocene, Fiji. Proposed as a subgenus of *Globularia* Swainson, 1840. Ladd (1977:27–28, pls. 7–9) reillustrated the type specimens and subsequently collected material which "shows the flaring aperture rim more clearly than do the types." *Waluina* Majima, 1989, error.

WALUINA Majima, 1989:26, 159. Error for *Waluia* Ladd, 1934.

WEXFORDIA Harmer, 1921:704. Type species *Wexfordia dautzenbergi* Harmer, 1921; monotypy [=*Torellia vestita* Harmer, 1918]. Pliocene, Great Britain. Wenz (1941:1037) placed this as a genus in the Polinicinae, but this is herein referred to the Trichotropidae.

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It must be noted that this bibliography contains only the primary sources; secondary sources are limited to those involving explicit discussion of a given genus or other aspects. Not included are the citations for homonyms (in other families) of naticid generic names as these can be readily obtained from the various editions of Neave (1939–1940 ff.). Also not included are citations to the original descriptions of the type species (unless, of course, they were described along with the new genus). To include these latter categories of references would needlessly lengthen this bibliography.

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AMPHIBIANS OF SOUTHEASTERN TANZANIA, WITH SPECIAL REFERENCE TO *STEPHOPAEDES* AND *MERTENSOPHRYNE* (BUFONIDAE)

J. C. POYNTON[1]

ABSTRACT. Records are given of 47 species of anurans collected in southeastern Tanzania. *Stephopaedes* and *Mertensophryne* are discussed at length; the two genera are provisionally regarded as being distinct on the grounds of differences in adult morphology, and diagnoses are given. Tanzanian material of *Stephopaedes* is described as a species distinct from the Zimbabwean *S. anotis*. *Mertensophryne m. micranotis* and *M. m. rondoensis* are found to be inseparable, and *schmidti* Grandison is excluded from this genus. *Stephopaedes* and *Mertensophryne* are apparently restricted to eastern African lowland forest and transitional lowland-Afromontane forest, now very fragmented. Most eastern Tanzanian species are assignable to an East African lowlands fauna, with characteristically enormous ranges. A set of widespread species with ranges centered more to the west is represented in more upland areas. There are relatively few endemic species.

INTRODUCTION

Southeastern Tanzania is here taken to be the region of Tanzania south of the Great Ruaha and Rufiji Rivers, and east of the highlands as demarcated by the 1,000 m contour. This area for the most part consists of the extensive Southeast Plateau, and a Coastal Hill Region (Berry, 1971). Alluvial lowlands occur along most of the northern limit. Rainfall in the region is in excess of 800 mm per annum (Berry, 1971), with the result that it is "a land closely covered, the cover varying from *miombo* woodland to light scrub" (Moffett, 1958: 220). The vegetation is characterized as "East African coastal mosaic" and "drier Zambezian miombo woodland" in the UNESCO/AETFAT/UNSO vegetation map (White, 1983). No portion of the Afromontane Region (*sensu* White, 1978) is included.

The area has been visited by several collectors, starting with Livingstone's expeditions of the 1860s, and followed notably by Loveridge, Ionides, and Rees. The material has been deposited mainly in the Museum of Comparative Zoology and the British Museum (Natural History). Much of this material was reviewed briefly by Poynton (1977), but subsequent taxonomic work in eastern and, especially, southern Africa (covered by Poynton and Broadley, 1985a, 1985b, 1987, 1988) calls for a more thorough review. In particular, southeastern Tanzania is the only region in Africa where small-sized bufonids currently assigned to *Mertensophryne* and *Stephopaedes* are now known to be sympatric. The taxonomy of these bufonids has become confused (Poynton and Broadley, 1988), making a detailed discussion appropriate in this paper.

As the area reviewed here includes the Selous Game Reserve, it is hoped that this paper will stimulate further study of the amphibian fauna of this still rather poorly investigated region. The paper is based on a reexamination of material in the Museum of Comparative Zoology and the British Museum (Natural History). The acronyms MCZ and BM are used in the text. Other acronyms used are: FMNH, Field Museum of Natural History, Chicago;

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[NMZB, Natural] History Museum of Zimbabwe, Bulawayo; ZMUC, Zoological Museum, University of Copenhagen. A response was not obtained from the National Museums of Kenya, Nairobi, regarding Tanzanian material reported by Loveridge (1955) to have been deposited there; this material is listed separately in the species lists.

The nomenclature adopted in this paper follows that of Frost (1985), apart from more recent published changes.

SYSTEMATIC LIST

FAMILY BUFONIDAE

Genus *Stephopaedes*

Stephopaedes Channing, 1978. Type by original designation: *Bufo anotis* Boulenger, 1907.

Channing (1978) based his monotypic genus on the then recently discovered tadpole of *Bufo anotis*, which he believed to be "strikingly different from all other *Bufo* tadpoles known worldwide" (1978:394). Knowledge of tadpoles of other African dwarf bufonids was at the time very poor; subsequently, the tadpole of *Mertensophryne micranotis* was shown by Grandison (1980) to be extraordinarily similar to the *S. anotis* tadpole. Grandison (1980) did note some differences between the *S. anotis* and *M. micranotis* tadpoles. She reported the presence of an infrarostrodont in *micranotis*, which was taken to contrast with the condition in *anotis*, described by Channing (1978:394) as "Infrarostrodont absent (or very reduced and not pigmented or keratinized)." But in twenty Gosner stage 34–35 *anotis* tadpoles recently collected by Broadley (NMZB 8452), the infrarostrodonts are well developed and blackened in all but one individual, where it is small, although strongly keratinized. Rostrodonts in *anotis* and *micranotis* do not differ at this stage. As Grandison has noted, the interrupted row of supraangular keratodonts in *anotis* is lacking in *micranotis*, and the rows of keratodonts are shorter in *micranotis;* but this seems related to the much smaller size of the *micranotis* tadpole, in conformity with the much smaller adult size (average length of stage 34–35 is 21 mm in *anotis*, 11 mm in *micranotis*). The "less pronounced and incomplete development of the 'crown'" reported by Grandison (1980:302) in the *micranotis* tadpole does not constitute a

striking difference between stage 34–35 tadpoles of both species, and could be attributed to the size difference. The difference in tail shape noted by Grandison is not well marked: the dorsal fin rises more steeply in stage 34 tadpoles (BM 1982.850) than is illustrated in her figure 3 of a *micranotis* stage 30 tadpole, and resembles the condition in *anotis*.

It seems clear that the discernable differences in external features of *anotis* and *micranotis* tadpoles of the same Gosner stage are minor, and cannot be taken in themselves as grounds for generic separation. Ecological features, whose importance Channing (1978) emphasized in the definition of genera, likewise provide no grounds for separating *anotis* from *micranotis* at the generic level. In separating *Stephopaedes* from *Bufo*, Channing (1978) placed emphasis on the finding that "*Stephopaedes anotis* is adapted to breed in forest pools . . . the tadpole is adapted by virtue of its crown to live in pools with low oxygen tensions" (Channing, 1978:396). Yet the work of Grandison (1980) and Grandison and Ashe (1983) shows the tadpole of *M. micranotis* to be similarly adapted. Evidence from tadpole morphology and ecology would, adopting Channing's generic criteria, therefore lead directly to placing *Stephopaedes* in the synonymy of *Mertensophryne*.

Yet, before taking such a step, evidence from adult morphology needs to be considered. In the following discussion, "*anotis*" is initially taken, in the original sense of *S. anotis*, to include material from southeastern Zimbabwe and adjoining Mozambique, as well as material from southeastern Tanzania, the latter material having been referred, with some reservations, to "*Bufo anotis*" by Loveridge (1955) and by Poynton (1977). Later in this paper, the Tanzanian material will be assigned to a separate species. This proposed separation at the species level will not affect the discussion of the validity of the genus.

The genus *Mertensophryne* was erected by Tihen (1960), who considered the diagnostic features to be: seven presacral vertebrae, separate sacrum and coccyx, extensively developed quadratojugals and palatines, and absence of the m. adductor longus. The presacral vertebrae of 39 *Stephopaedes* specimens have been examined by means of clearing and staining, dissection, and X rays. Eight presacral vertebrae have been found in each case, although considerable variation is shown in the separation of the transverse processes of the eighth vertebra and the sacrum, to the extent that the structures are closely applied on the one side of one specimen (NMZB 8505). But as the number of presacral vertebrae is seven or eight in the *M. micranotis rondoensis* type series (Grandison, 1978), a count of presacral vertebrae does not produce satisfactory characters.

In *Stephopaedes* the sacrum and coccyx are separated in specimens that have been cleared and stained, dissected, and where X-ray images are clear; but Grandison (1978) has reported much variation in this part of the skeleton of *Mertensophryne*, which once more leads to limited taxonomic usefulness.

The quadratojugals and palatines of *anotis* match Tihen's description of being "extensively developed"; in fact they are even more developed than they are in *micranotis:* the palatine, pterygoid, and quadratojugal form a continuous unit supporting the maxilla, and the quadratojugal is developed to the extent of cradling the maxilla in a deep groove, which is continued by a groove in the pterygoid. Support for the maxilla is continued by a flanged expansion of the palatine. The whole structure is further supported by the medial rami of the pterygoid being applied to the parasphenoid alae: in *micranotis*, the medial rami are very reduced, falling far short of the parasphenoid rami. This degree of development in *anotis*, especially the groove in the quadratojugal securing the end of the maxilla, is unusual; it possibly compensates for reduced ossification of the descending arm of the squamosal, noted by Grandison (1981), as well as for the

generally more robust skull, which indeed shows some ornamentation of the nasals, frontoparietals, and dorsal portion of the squamosal. The skull of *anotis* therefore appears to be substantially different from that of *micranotis*.

Regarding the m. adductor longus, the absence of which was taken by Tihen to be a feature of *Mertensophryne*, in *anotis* the muscle varies from being clearly lacking (which seems the usual state) to being present as a well-defined strip of muscle that leaves the anterior edge of the m. pectineus and joins the connective tissue sheath of the m. adductor magnus. As in the case of vertebral features, therefore, variation does not permit a clear separation between the two genera to be made on the basis of this character.

While most internal features selected by Tihen for diagnosing *Mertensophryne* therefore do not decisively exclude *anotis*, a number of differences seem noteworthy in the external features of the adults of the two. Particularly evident are the parotid glands of *anotis*, which are much wider than the width of the upper eyelid, and descend laterally to the level of the arm. In *micranotis* these glands are weakly developed, are narrower than the width of the upper eyelid, and have straight lateral edges. While much variation in the development and shape of the parotid glands is conventionally accepted within the genus *Bufo*, the condition in *Stephopaedes* seems to be unique. Other external features distinguishing *Mertensophryne* from *Stephopaedes* (and dwarf African toads in general) are: marked glandular swellings in the canthal region; shortened outer toe, reaching only halfway or less along the length of the proximal digit of the fourth toe; no distinct webbing between toes; large, well-separated, conical, and heavily keratinized spines on the first finger of breeding males; small spines present on the rim of cloacal tube in breeding males; males with cornified dorsal spines (skin of males is typically smoother than female skin in African dwarf bufonids, including *Stephopaedes*). Markings in *Mertensophryne* and *Stephopaedes* are radically different: as will be described below, a middorsal inverted V posterior to the occipital region is the commonest dark marking in *Stephopaedes*, whereas *Mertensophryne* has a longitudinally arranged pair of parallel stripes in this region.

Putting the available data together, it appears that *Stephopaedes* and *Mertensophryne* are primarily sylvicolous bufonids that oviposit in water-filled holes, such as between buttress roots, or treeholes, or snail shells (Grandison, 1980; Grandison and Ashe, 1983; Poynton and Broadley, 1988). This allows breeding to occur where surface water does not accumulate or flow for long above soil, a situation not uncommon in eastern African forests. In these forests, it may be noted, microhylid and arthroleptid terrestrial breeders tend to be major elements of the anuran fauna. The ecological adaptation of these bufonids is indicated morphologically by highly derived tadpole features, and by the possession of a cloacal tube which is deeply folded and which directs the vent markedly towards the ventral surface, a character likely to be associated with internal fertilization (Grandison and Ashe, 1983; Poynton and Broadley, 1988). Yet, as noted above, there appears to be considerable divergence in several adult features, which provide *Stephopaedes* and *Mertensophryne* each with some unique character states. Notable among these are: the presence in *Stephopaedes* of a particularly strong posterior maxillary support, the slightly exostosed roofing of the skull, and the broad, flattened parotid glands; in *Mertensophryne* the reduced outer toe, the large spines on the inner finger of the breeding male, and the generally more spiny condition of the male. Two diverging phyletic lines are therefore indicated by adult morphology.

This situation may be accommodated nomenclaturally by recognizing separate genera: *Stephopaedes* and *Mertensophryne*. Therefore, despite what is implied

by Channing's views, the present paper takes a conservative position of recognizing two separate genera, pending more complete ecological and morphological knowledge of African dwarf toads. Sight should not be lost of the fact that the life histories of many African dwarf toads are still unknown or very imperfectly known. Regarding morphological features, account has to be taken of complexities in the diagnosis of *Mertensophryne*, discussed below; account also has to be taken of the uncertain generic status of forms such as *Bufo melanopleura* Schmidt and Inger, and indeed, the very poor definition of *Bufo* as a whole.

For the time being, *Stephopaedes* may be characterized as possessing the following combination of characters. (1) Tadpoles with a "crown" of tissue encircling the eyes and nostrils, no gap in the mental papillae, possessing supra- and infrarostrodonts and four rows of keratodonts (supra-angular row interrupted). (2) Adults medium sized, distance from snout to urostyle tip in females up to 45 mm, males to 38 mm. (3) Eight presacral vertebrae; separate sacrum and coccyx with bicondylar articulation. (4) Large quadratojugal cradling the maxilla in a groove; palatine robust and prominently ridged. (5) Nasals, frontoparietals, and squamosals slightly exostosed. (6) Descending arm of squamosal not ossified, to ossified halfway down. (7) Medial ramus of pterygoid applied to parasphenoid, overlapping in anterior-posterior plane. (8) No columella or tympanum. (9) No, or only vestigial, m. adductor longus; well-developed m. tensor fasciae latae, inserting on m. cruralis at about one-third of its length. (10) Ovarian eggs reaching a size of 2.5 mm, pigmented at one pole, numbering about 85 per gravid female. (11) Opening of vent directed very markedly towards the ventral surface in both sexes, and lined by deeply folded integument, deep folding also present in lining of cloacal tube. (12) Breeding males with minute asperities on inner and upper surfaces of inner two fingers, occasionally also on inner palmar tubercle. (13) No tarsal fold. (14) Subarticular tubercles of fingers and toes doubled, two enlarged palmar tubercles present (but inner much smaller and may be only slightly larger than other palmar tubercles). (15) Toes with limited webbing; one to two phalanges of third toe free. (16) Outer toe extending beyond proximal phalanx of fourth toe. (17) Parotid glands considerably wider than width of upper eyelid, flattened, extending ventrally to level of upper jaw. (18) Dorsal skin of females with light-tipped spines that surmount warty bases, the larger warts bearing rosettes of spines; ventral surface with more densely packed spines, but not forming well-developed rosettes. Skin of males less spinose. Spines on individuals below length of about 32 mm tend to have pointed, keratinized tips. (19) Dark dorsal markings often lacking, especially in Zimbabwean material. A dark middorsal spot behind the occipital region is the most common marking, typically forming the apex of an inverted V whose arms follow the diverging inner margins of the parotid glands. Dark interorbital patches or a bar may be present, and sometimes a pair of sacral patches. Remaining areas over back may show relative lightening, especially in the parotid and sacral regions.

Stephopaedes differs from *Mertensophryne* notably in having wide parotid glands; toes with webbing; outer toe extending beyond proximal phalanx of fourth; breeding males with a dense covering of minute asperities on two fingers; quadratojugal possessing a deep groove into which the maxilla is slotted; medial ramus of pterygoid making contact with the parasphenoid; and in showing cranial exostosis, which is apparently unique among small-sized African bufonids. Differences in markings and in size may also be noted.

Turning now to variation within *Stephopaedes*, Loveridge (1955) and Poynton (1977) assigned southeastern Tanzanian material to *anotis* Boulenger, while remarking on some differences between this material and material from the type lo-

cality of *anotis* in southeastern Zimbabwe. Loveridge stated that ventral markings were lacking in the single specimen he had from Tanzania (although he noted that ventral markings showed variation in Zimbabwean material), while Poynton recorded differences in webbing, head width, and dorsal markings between Tanzanian and Zimbabwean material. Subsequently, more material has been examined from Chirinda Forest, the type locality of *anotis* in Zimbabwe, and from the nearby Dombe Forest in Mozambique; and more material from southeastern Tanzania has been examined in the Museum of Comparative Zoology and the British Museum (N. H.). The increased amount of material has revealed consistent differences between Zimbabwe–Mozambique and Tanzanian collections. In view of this, Poynton and Broadley (1988) restricted the acceptable range of *S. anotis* to southeastern Zimbabwe and adjoining Mozambique. The Tanzanian material requires a new name. It is here named to honor the memory of the late Arthur Loveridge, who first reported this form in Tanzania, and who made an unequalled contribution to the herpetology of East Africa. In honoring his memory, recognition is given to the support that the Museum of Comparative Zoology gave to Loveridge, and also the assistance that the museum has continued to give to subsequent work on eastern and southern African amphibians.

Stephopaedes loveridgei new species
Figures 1, 2

Bufo anotis, not Boulenger, 1907. Loveridge, 1955: 195; Poynton, 1977:39.

Holotype. A gravid female from Mahenge, Tanzania (8°41′S, 36°43′E, ca. 1,000 m) in the British Museum (Natural History), London (BM 1969.1492), collected at an unspecified date in 1964 by A. Rees.

Paratypes. Six specimens (a 39 mm female which has been cleared and stained with alizarin, and five juveniles) in the British Museum (N. H.) (BM 1969.1493 through 1969.1498) collected by Rees between 1963 and 1964 from Mahenge. The specimen cited by Loveridge (1955) is also regarded as a paratype: a female with immature ova in the Museum of Comparative Zoology (MCZ 27907) collected by C. J. P. Ionides from "Kilwa" (?Kilwa Kivinje, 8°45′S, 39°24′E), 25.viii.1950.

Other material. Five half-grown specimens (MCZ 29430 through 29434) collected by C. J. P. Ionides from Liwale (9°48′S, 37°56′E), 13 to 16.v.1957. One juvenile (BM 1988.184) from the Rondo Plateau (ca. 10°08′S, 39°12′E) collected by A. Braunlich, 13.xi.1988, and two gravid females (BM 1988.246 through 247) from Kiwengoma Forest Reserve (ca. 8°20′S, 38°56′E) collected by J. Kingdon, probably in 1989.

Diagnosis. Closely resembling *Stephopaedes anotis* (Boulenger, 1907), but differing therefrom in the reduced webbing (two phalanges of third toe free in *loveridgei*, one free in *anotis*); relatively smaller outer metatarsal tubercle (0.75 or less length of inner metatarsal tubercle in *loveridgei*, more than 0.75 length in *anotis*). Adult dorsal skin (at least of females) more spinose than in *anotis*, e.g., >45 spines on upper eyelid of *loveridgei* (<35 in *anotis*), clear rosettes of spines on upper surfaces of hind limbs of *loveridgei*, although weakly developed in the Kiwengoma Forest Reserve specimens (not developed in *anotis*). Covering of minute spines on lip of vent more strongly developed than in *anotis*. Dorsal markings usually strongly defined in *loveridgei* (weakly or not shown in *anotis*), while ventral markings are very reduced or absent (ventral freckling nearly always well developed over pectoral region in *anotis*).

Loveridge (1955) noted that the Kilwa specimen differed from typical *anotis* in lacking ventral markings; it also differs from *anotis* in the other characters listed in the diagnosis of *loveridgei*. Poynton (1977) distinguished Tanzanian from Zimbabwean material partly on the basis of a supposedly broader head in the former.

Figure 1. *Stephopaedes loveridgei* sp. n. Dorsal aspect of holotype BM 1969.1492, from Mahenge, Tanzania. Natural size.

Figure 2. *Stephopaedes loveridgei* sp. n. Dorsal aspect of paratype BM 1969.1493, from Mahenge, Tanzania. Natural size.

The currently available material shows allometry in the head width/body length relationship, the head becoming relatively narrower the longer the specimen (average head width/body length 37.5% at length of 27 mm, 35.5% at length of 37 mm). Tanzanian and Zimbabwean material form a single regression line.

Description of type material. Showing the features of the genus, as discussed above. Two phalanges of third toe free of main webbing, although edge of web very serrated, making determination imprecise. Outer metatarsal tubercle rounded, 0.75 or less length of inner. Adult dorsal skin (known only from females) densely covered with light-tipped spines which surmount small, warty bases; larger warts over lateral and urostylar areas and on dorsal surfaces of legs have rosettes of spines, otherwise the spines are single. Dense covering of minute conical asperities conspicuous on the lip of the vent, even in immature specimens of both sexes.

Markings (in alcohol): top of head, parotid glands and central region of back a light brown; darker brown laterally. A dark middorsal V-shaped marking in the scapular region, apex pointing anteriorly, arms usually continuing posteriorly to mark the inner margins of the parotid glands. Also a thin, often broken, dark interocular bar, and a pair of darker sacral spots. A fine light line overlying the urostyle. Dorsal markings are faintly shown in the holotype; the paratypes show the sacral, scapular, and interocular markings more clearly (Fig. 2). Ventral surface immaculate or with a single, elongated dark fleck in the anterior pectoral region. There are no regular ventral markings, nor the freckling typical of *S. anotis*.

Dimensions of holotype: body length from tip of snout to tip of urostyle 37.8 mm, body length from snout to vent 41.8 mm (specimen well hydrated), width of head 14.3 mm, length of tibia (folded) 14.9 mm, length of foot (including metatarsal tubercle) 13.9 mm. BM paratype 1969.1494 has a snout–urostyle length of 38.4 mm, head width of 13.6 mm; the remaining BM paratypes have a snout–urostyle length ranging from 26.9 mm to 31.2 mm. The MCZ paratype from Kilwa has a snout–urostyle length of 32.2 mm, head width of 12.6 mm.

Snout–urostyle lengths of other material: Liwale 24.1–29.5 mm, Rondo Plateau 30.4 mm, Kiwengoma Forest Reserve 34.3–35.0 mm.

Discussion. Males in breeding condition have yet to be described. As with *S. anotis*, and most African dwarf toad species, adult

males may be expected to have smoother skins than females. Digital asperities in breeding condition may be expected to be numerous and minute. The ovarian eggs in the holotype have a diameter of 2.5 mm, which is the same size as ovarian eggs in *anotis* (Poynton, 1964a). It can be expected that the course of development of the tadpole is similar to that of *anotis*. In view of the lack of detailed knowledge of the behavior of *anotis* adults, the relatively limited webbing of *S. loveridgei* adults cannot lead to very firm predictions about habitat preferences in this species. Loveridge (1955) reported that the Kilwa specimen was "taken during dry weather at the edge of a small lake." The *loveridgei* specimens from Mahenge were collected by Rees in "semi-montane type country" rising out of "*Pseudoberlina/Brachystegia* country" (Rees, pers. comm., 1963). It may be hoped that the new BM material will stimulate the gathering and publication of more ecological data.

As will be discussed under the zoogeographical section, the disjunct distribution pattern shown by *Stephopaedes* is not without parallel in forested regions of eastern Africa. Whether distributional gaps shown by upland and/or sylvicolous taxa are products of range retraction associated with Quaternary climatic cycles, or whether the gaps originate from some form of dispersal, has been a matter of debate among African biogeographers (Poynton, 1983, 1986), which still continues owing to the limited amount of relevant data (e.g., Harmsen, 1989). While the present taxonomic differentiation in *Stephopaedes* appears at first sight to be the result of vicariance, there is too little information regarding both the environmental history of southeastern Africa, and the phyletic history of African dwarf bufonids, to test a vicariance hypothesis.

Genus *Mertensophryne*

Mertensophryne Tihen, 1960. Type by original designation: "*Bufo (micranotis) rondoensis* Loveridge, 1942."

Tihen (1960) chose *Bufo micranotis rondoensis* as the type of *Mertensophryne;* he referred *M. m. micranotis* Loveridge (1925) to *Mertensophryne* only tentatively, as no specimens of this form were examined. Tihen also referred *Bufo ushoranus* Loveridge (1932) to *Mertensophryne,* seemingly in error, since Grandison (1972) has shown this taxon to be a synonym of *B. taitanus* Peters. Tihen evidently based his conception of *B. ushoranus* on material from the Upemba Park, Zaire, which was misidentified as *ushoranus* by Schmidt and Inger (1959) and subsequently renamed *Mertensophryne schmidti* by Grandison (1972). Improved knowledge of the morphology and ecology of East African dwarf bufonids, notably through the work of Grandison (1972, 1978, 1980), shows Tihen's diagnosis of *Mertensophryne* to be inadequate, and consequently raises questions about the correctness of his inclusion of *schmidti* (as *ushoranus*) in the genus.

There are in fact several features that distance *schmidti* from *micranotis:* large single palmar tubercle; outer toe not markedly reduced; very spinose skin, with ventral as well as dorsal rosettes; nuptial asperities consisting of clusters of very small horn-tipped spinules; cloacal opening not markedly directed ventrally; ova unpigmented. Grandison (1978) noted the presence of an accessory head to the m. adductor magnus of *schmidti,* lacking in *micranotis,* and, in correspondence, has drawn attention to extensive anterior development of the sphenethmoid, which, quite unlike the sphenethmoid of *micranotis,* reaches the palatal processes of the premaxillae. In correspondence she has also drawn attention to the presence of a vestigial columella in one of the *schmidti* paratypes (BM 1977.1211, which has been cleared and stained with alizarin), and to the presence of small eustachian tubes. These features have been confirmed by the present writer.

In external features, *schmidti* in fact shows closer resemblance to the sympatric

Bufo melanopleura Schmidt and Inger than to *micranotis*, notably in the single enlarged palmar tubercle, enlarged metatarsal tubercles, outer toe not reduced, presence of webbing, densely spinose skin, cloacal opening directed more posteriorly than ventrally, small eustachian tube openings. It is not suggested here that *schmidti* and *melanopleura* should be assigned together to a separate genus. The current lack of knowledge of the larval stages of *schmidti* and *melanopleura* is a particular obstacle to an elucidation of their phylogenetic position. Accordingly, *schmidti* is here assigned along with *melanopleura* to *Bufo* (in its currently loose sense); it then has the combination *Bufo schmidti* (Grandison, 1972), with the synonyms *B. ushoranus* Schmidt and Inger, 1959 (not Loveridge, 1932), *Mertensophryne ushoranus* Tihen, 1960, and *Mertensophryne schmidti* Grandison, 1972.

Mertensophryne is therefore considered here to include only one species, *micranotis* Loveridge, with a known distribution in eastern Kenya and Tanzania. The genus may be characterized by possessing the following combination of characters. (1) Tadpoles with a "crown" of tissue encircling eyes and nostrils, no gap in the mental papillae, possessing supra- and infrarostrodonts and three rows of keratodonts. (2) Adults small sized (snout to urostyle tip in gravid females 16 to 24 mm, mature males 16 to 22 mm). (3) Seven, occasionally eight, rarely six, presacral vertebrae; sacrococcygeal articulation usually monocondylar, occasionally bicondylar, rarely fused. (4) Quadratojugal long, extending length of pterygoid fossa, overlapped by the maxilla; palatine slender, lacking any pronounced ridge. (5) No cranial ornamentation. (6) Descending arm of squamosal not ossified. (7) Medial ramus of pterygoid very reduced, not making contact with parasphenoid. (8) No columella or tympanum. (9) No m. adductor longus; well-developed m. tensor fasciae latae. (10) Ovarian eggs reaching a size of 2 mm, faintly pigmented at one pole, numbering about 76 per gravid female. (11) Opening of vent directed very markedly towards the ventral surface in both sexes, and lined by deeply folded integument, deep folding also present in lining of cloacal tube; cloacal opening of breeding males with transitory spines. (12) Breeding males with large, well-separated, heavily keratinized nuptial spines. (13) No tarsal fold. (14) Subarticular tubercles of fingers and toes doubled, two enlarged palmar tubercles present (inner smaller and may be only slightly larger than other palmar tubercles). (15) Toes without definite webbing. (16) Outer toe reaching only halfway or less along proximal phalanx of fourth toe. (17) Parotid glands weakly developed, narrower than upper eyelids, outer edge straight. (18) Dorsal skin of males and females with minute, light-tipped spines surmounting small warts, only rarely forming rosettes; ventral surface with smooth, pavement-like warts, more columnar over posterior area. (19) Dorsal markings: dark, slightly raised areas which, when most complete, form a middorsal stripe on the snout, an oblique stripe over each eyelid, a patch between the posterior region of the eyelids, and three pairs of parallel, longitudinally arranged stripes in the occipital, postscapular and postsacral regions, the latter pair tending to become rounded as patches. Light patches may occur in the occipital area, and more commonly a pair of light sacral patches is developed, sometimes joining middorsally and continuing into a lightening of most of the area between the dark longitudinal stripes. A middorsal dark inverted V behind the occipital area, found in *Stephopaedes*, is not developed.

In the current poor state of knowledge of small-sized African bufonids, it cannot be said that *Stephopaedes* and *Mertensophryne* are more closely related to each other than either is to any other bufonid. Dubois (1986) has however grouped *Schismaderma* with *Stephopaedes* and *Mertensophryne* in a "tribe" mainly on account of perceived similarities between

structures on the dorsal surface of the tadpoles. The *Schismaderma* tadpole has a horseshoe-shaped fold extending from above the eyes to the trunk, and not enclosing the nostrils (Charter and MacMurray, 1939); whereas in *Stephopaedes* and *Mertensophryne* the "crown" encircles both nostrils and eyes. No homology in these structures can be maintained. Differences between the "saddle" of *Schismaderma* and the "crown" of *Stephopaedes* are shown clearly in the recent illustrations by Lambiris (1989).

Dubois also placed weight on Grandison's (1981) report of reduction in ossification of the squamosal in a "*vertebralis* group, which includes *Stephopaedes*, *Mertensophryne*, and possibly also *Schismaderma*" (pp. 208–209). The tentativeness expressed here regarding *Schismaderma* provides no grounds for supposing homology: indeed, Grandison (pers. comm., 1988) considers the squamosal in *Schismaderma* to be a "slender triradiate element that, in shape, is unique among the African bufonids." Taking into account the very marked differences between *Schismaderma* and the other two genera in egg size and number, and the tadpole and adult structure, behavior, and ecology, an exclusive grouping of *Schismaderma*, *Stephopaedes*, and *Mertensophryne* seems misconceived.

The "*vertebralis* group," which Grandison (1981:208) saw as including "all the medium and small sized toads that have double subarticular tubercles and occur in southern and eastern parts of Africa," contains many species that are still too poorly known to allow a phyletic analysis of the group. At the same time, new work is revealing variation—even within a single series of individuals—in features that at one time were taken to be definitive or diagnostic, such as the number of presacral vertebrae, the postsacral articulation, and the occurrence of the m. adductor longus. It seems premature at the moment to attempt to identify sister groups of *Stephopaedes* and of *Mertensophryne*. Such groups could be looked for among earless members of the large "*vertebralis* group" with two palmar tubercles, such as *Bufo lonnbergi* Andersson (Grandison, 1972; Poynton and Broadley, 1988). This is primarily a sylvicolous form. It is of possible significance that males of this species emit a mating call, even though otic structures are lacking (Tandy and Keith, 1972): the same is reportedly true of *Stephopaedes* and *Mertensophryne* (FitzSimons, 1939; Grandison and Ashe, 1983). *B. lonnbergi* has *Bufo*-like eggs and tadpoles, however (Stewart, 1967; Grandison, 1972).

Turning now to variation within *Mertensophryne*, Loveridge (1942) described *M. micranotis rondoensis* from just south of 10°S, separating it from the more northern *M. m. micranotis* "only in the throat being almost entirely white in the entire series, whereas in both sexes of *micranotis* . . . the throat is so heavily overlaid with black as to appear black." The *rondoensis* type series shows variation in gular pigmentation, and the presence of up to seven large flecks is not consistent with the description "almost entirely white." The throat of the holotype of *m. micranotis* is in turn not wholly pigmented. BM material from Pugu Forest, near Dar es Salaam (ca. 7°S), and from the Kiwengoma Forest Reserve, south of Utete (ca. 8°S), shows much variation in throat markings. Particularly notable is the variation shown in the four Kiwengoma F. R. specimens (BM 1988.242 through 245), collected about 230 km north of the type locality of *m. rondoensis:* the throat varies from being densely pigmented to being lightly flecked. In a specimen collected recently from the Rondo Plateau (BM 1988.184), five large flecks are present. It could hardly be said that there are clear indications even of a north-south cline in this feature, with the result that Loveridge's separation based on throat markings seems unworkable.

The *m. rondoensis* types are separable from the *m. micranotis* types on the basis of the minute size of their metatarsal tubercles, the diameter being less than the

width of the toe tips: in the *micranotis* types the diameter is greater than the diameter of the toe tips. MCZ and BM material from Zanzibar Island and from Kenya agree with *micranotis* in this respect. In the Pugu Forest material, recorded by Howell (1979, 1981) as *m. rondoensis*, the diameters of the tubercles and toe tips are about equal, while in the Kiwengoma F. R. series the diameter of the tubercles varies from being equal to being less than the diameter of the toe tips. A north-south cline therefore appears to be indicated in the relative size of the metatarsal tubercles, but it does not offer clear grounds for separating *m. rondoensis* from *m. micranotis*. A north-south cline may also exist regarding adult size: the snout–urostyle tip length is, so far, not known to exceed 18.2 mm in Rondo Plateau females, while Kenyan females may attain a length of 22 mm. The Kiwengoma F. R. series reaches a length of 19.5 mm. This again provides no means for clearly separating *m. rondoensis* from *m. micranotis*. No other features have been discerned that suggest any justification for retaining Loveridge's *rondoensis*.

Mertensophryne micranotis (Loveridge)

Bufo micranotis Loveridge, 1925:770.
Bufo micranotis rondoensis Loveridge, 1942:387. Tihen, 1960:266.

Records. Nchingidi, 823 m, "the name given to a clearing at the [Rondo] forest edge" (Loveridge, 1944) (MCZ), Rondo Plateau (BM), Kiwengoma Forest Reserve (BM).

Genus *Bufo*

Bufo Laurenti

Bufo gutturalis Power

Bufo gutturalis Power, 1927.
Bufo regularis, not Reuss, 1833. Loveridge, 1942:385; 1951:203; 1955:195. Poynton, 1977:39.

Records. Kilwa (MCZ), Kitaya (MCZ), Kivukoni (BM), Lindi (MCZ), Mahenge (BM), Mikindani (MCZ), Mtilangondo (BM), Rufiji River (7°47′S, 38°14′E) (BM). Liwale (Loveridge, 1955).

Bufo maculatus Hallowell

Bufo maculatus Hallowell, 1855 "1854."
Bufo pusillus Mertens, 1937. Poynton, 1977:39.

Records. Luwegu (BM), Mahenge (BM).

Bufo reesi Poynton

Bufo reesi Poynton, 1977:37.

Record. Merera (BM).

Bufo lindneri Mertens

Bufo lindneri Mertens, 1955. Clarke, 1989:298.

Record. Liwale District (BM).

Genus *Schismaderma*

Schismaderma Smith, 1849.

Schismaderma carens (Smith)

Bufo carens Smith, 1848. Loveridge, 1951:202; 1955: 195.

Records. Liwale (BM, MCZ).

FAMILY MICROHYLIDAE

Genus *Breviceps*

Breviceps Merrem, 1820.

Breviceps mossambicus Peters

Breviceps mossambicus Peters, 1854. Loveridge, 1942: 434. Poynton, 1977:39.

Records. Kilwa dist. (BM), Mahenge (BM), Mikindani (MCZ), Nchingidi (MCZ).

Genus *Phrynomerus*

Phrynomerus Noble, 1926.

Phrynomerus bifasciatus bifasciatus (Smith)

Brachymerus bifasciatus Smith, 1847.
Phrynomerus bifasciatus (Smith). Loveridge, 1942: 435; 1951:204; 1955:197. Poynton, 1977:39.

Records. Ifakara (BM), Kilwa (MCZ), Lindi (MCZ), Mahenge (BM). Liwale (Loveridge, 1955).

Genus *Spelaeophryne*

Spelaeophryne Ahl, 1924.

Spelaeophryne methneri Ahl

Spelaeophryne methneri Ahl, 1924. Loveridge, 1942: 434; 1955:197. Poynton, 1977:39.

Records. Litumba (MCZ), Mahenge (BM, NMZB), Matumbi (type locality: types not traced), Nchingidi (MCZ). Liwale (Loveridge, 1955).

FAMILY RANIDAE

Genus *Pyxicephalus*

Pyxicephalus Tschudi, 1838.

Pyxicephalus adspersus edulis Peters

Pyxicephalus edulis Peters, 1854.
Rana adspersa edulis (Peters). Loveridge, 1951:204; 1955:197.
Pyxicephalus adspersus, not Tschudi, 1838. Poynton, 1977:39.

Records. Kitaya (MCZ), Kivukoni (BM), Lindi District (MCZ), Mahenge (BM), Mikindani (MCZ), Tunduru (MCZ).

Discussion. Poynton and Broadley (1985b) tentatively accepted Parry's (1982) division of *P. adspersus* into three subspecies "until variation over the whole African range has been thoroughly investigated." In the material listed above, the ratio head width/snout–urostyle tip length varies from 50% (MCZ 25372, Kitaya) to 40% (BM 1969.1400, Kivukoni), a range which spans the ratios of all three supposed forms. This variation correlates with variation in pectoral markings to the extent that these markings tend to appear in material with relatively narrow heads, but they also occasionally appear in specimens with a width/length ratio of up to 44%, contrary to the <41% allowed in the diagnosis of *adspersus angusticeps* by Parry (1982) and Poynton and Broadley (1985b). These markings in southeastern Tanzanian juveniles are not as well developed as in the *adspersus angusticeps* type series from Beira. Regarding more northern Tanzanian material, it may be noted that MCZ 25379 from Amboni has a width/length ratio of 39% and well-developed gular and pectoral marking, placing it technically in *angusticeps*. This record seems geographically as anomalous as the "Shire Highlands" record reported in Poynton and Broadley (1985b). MCZ 59506 and 59507 from near Tabora, on the other hand, have some pectoral marking yet have width/length ratios of 47% and 49%, which are at the *a. adspersus* end of the *a. edulis* range. This is also true of MCZ 59395 from Kizumbe.

The light tympanic marking typical of *edulis* is not present in some specimens in the middle of the *edulis* width/length range (e.g., BM 1969.1402 and 1403 from Mahenge). Overall, it seems that this Tanzanian material does not give effective support to Parry's taxonomic analysis, and the assignation of the specimens listed above to *a. edulis* has again to be tentative.

Genus *Rana*

Rana Linnaeus, 1758.

Rana angolensis Bocage

Rana angolensis Bocage, 1866. Poynton, 1977:39.

Records. Kivukoni (BM), Mahenge (BM).

Genus *Hylarana*

Hylarana Tschudi, 1838.

Hylarana galamensis (Duméril and Bibron)

Rana galamensis Duméril and Bibron, 1841.
Limnodytes bravanus Peters, 1882.
Rana galamensis bravana (Peters). Loveridge, 1955: 196.
Hylarana galamensis bravana (Peters). Poynton, 1977: 39.

Records. Kihanzi/Kilombero (BM), Kilwa (MCZ).

Genus *Hildebrandtia*

Hildebrandtia Nieden, 1907.

Hildebrandtia ornata ornata (Peters)

Pyxicephalus ornatus Peters, 1878.
Rana ornata ornata (Peters). Loveridge, 1951:204; 1955:196.

Hildebrandtia ornata ornata (Peters). Poynton, 1977: 39.

Records. Kilwa (MCZ), Kivukoni (BM), Lindi District (MCZ), Liwale District (BM).

Genus *Ptychadena*

Ptychadena Boulenger, 1917.

Ptychadena oxyrhynchus (Smith)

Rana oxyrhynchus Smith, 1849.
Ptychadena oxyrhynchus (Smith). Poynton, 1977:39.

Record. Mkomangasha (BM).

Ptychadena anchietae (Bocage)

Rana anchietae Bocage, 1867.
Rana oxyrhynchus oxyrhynchus, not Smith, 1849. Loveridge, 1942:416; 1951:204; 1955:196.
Rana mascareniensis mascareniensis, not Duméril and Bibron, 1841. Loveridge, 1955:196 (part: MCZ 27918).
Ptychadena superciliaris, not Günther, 1848. Poynton, 1977:39.

Records. Boma Ulanga (BM), Ifakara (BM), Kilwa (MCZ), Lindi District (MCZ), Mahenge (BM), Mbanja (MCZ), Mikindani (MCZ), Shughuli (BM), Tunduru (MCZ).

Ptychadena mascareniensis mascareniensis (Duméril and Bibron)

Rana mascareniensis Duméril and Bibron, 1841. Loveridge, 1942:417; 1955:196.
Ptychadena m. mascareniensis (Duméril and Bibron). Poynton, 1977:39.

Records. Boma Ulanga (BM), Kitaya (MCZ), Kivukoni (BM).

Ptychadena taenioscelis Laurent

Ptychadena taenioscelis Laurent, 1954. Poynton, 1977:39.
Rana mascareniensis mascareniensis, not Duméril and Bibron, 1841. Loveridge, 1951:204 (MCZ 26642).

Records. Ikulia (BM), Liwale (MCZ), Mkomangasha (BM).

Ptychadena mossambica (Peters)

Rana mossambica Peters, 1854.
Rana mascareniensis uzungwensis, not Loveridge, 1932. Loveridge, 1955:196.
Rana ansorgei, not Boulenger, 1905. Loveridge, 1955: 196.
Ptychadena upembae upembae, not Schmidt and Inger, 1959. Poynton, 1977:40.

Records. Kilwa (MCZ), Liwale (MCZ), Mbega (BM), Tunduru (MCZ).

Discussion. The Mbega specimen (BM 1969.1398) was assigned with some doubt to *upembae* rather than to *mossambica* by Poynton (1977) on the grounds of its relatively long feet. In other respects it does not agree with the current diagnosis of *upembae* (Poynton and Broadley, 1985b). The foot length in Mozambican material of *mossambica* rarely reaches 51% of the body length (snout–urostyle tip); the maximum is an exceptional 54% shown by a BM specimen from Caia, and also by the lectotype from Cabaceira, discussed by Poynton (1966). The feet of the Mbega specimen are 55% of the body length. This value falls within the range of *P. gansi* Laurent from Somalia, which is 53% to 57%. This range is also shown by BM material from the Kenyan lowlands. Lanza (1983) believes *gansi* to be "probably a synonym of *P. mossambica*," and this view would be supported if a cline in foot/body length between Kenya and Mozambique were to be demonstrated. The small amount of Tanzanian material listed above does indeed suggest the existence of an intermediate range of variation in that area. The MCZ specimen from Kilwa referred tentatively to *upembae* rather than to *mossambica* by Poynton (1977), on account of its relatively long feet, has a foot/body length of 52%, which is not unexpected for *mossambica* of southeastern Tanzania.

Somalian and Kenyan material agreeing with *gansi* differs from Mozambican material not only in foot length, but also to some extent in the markings on the hinder surface of the femur. Clear banding is usual in northern material; in southern material an irregular mottling is usual, but some individuals—including the *mossambica* lectotype (Poynton, 1966)—show distinct banding. Such individuals do not necessarily show the *gansi* character of longer feet: for example a specimen in a BM series from Beira has banded femora but a foot

length of 46% body length. The Mbega specimen shows irregular banding.

It seems likely that accumulating material will make it increasingly difficult to distinguish clearly between *mossambica* and *gansi*. The material listed above is accordingly assigned to *mossambica*.

Genus *Phrynobatrachus*

Phrynobatrachus Günther, 1862.

Phrynobatrachus natalensis (Smith)

Stenorhynchus natalensis Smith, 1849.
Phrynobatrachus natalensis (Smith). Poynton, 1977:39.

Records. Mahenge (BM), Msolwa River (BM), Ruaha River (BM).

Phrynobatrachus acridoides (Cope)

Staurois acridoides Cope, 1867.
Phrynobatrachus acridoides (Cope). Loveridge, 1942:421; 1955:197. Poynton, 1977:39.

Records. Boma Ulanga (BM), Ikulia (BM), Kisanga (BM), Kitaya (MCZ), Luwegu (BM), Mahenge (BM), Mbega (BM), Mikindani (MCZ), Ruaha River (BM), Uga (BM). Tunduru (Loveridge, 1955).

Phrynobatrachus mababiensis FitzSimons

Phrynobatrachus mababiensis FitzSimons, 1932.
Arthroleptis minutus, not Boulenger, 1895. Loveridge, 1942:425.
Phrynobatrachus ukingensis mababiensis FitzSimons. Poynton, 1977:39.

Records. Lindi (MCZ), Maji ya Moto (BM), Mikindani (MCZ), Mwaya (BM), Riva Lumango (BM).

Discussion. This material shows some variation in the dilation of the tips of the toes, but it falls within the range of variation shown by a large MCZ series from Dar es Salaam, discussed by Poynton and Broadley (1985b:168).

FAMILY RHACOPHORIDAE

Genus *Chiromantis*

Chiromantis Peters, 1854

Chiromantis xerampelina Peters

Chiromantis xerampelina Peters, 1854. Loveridge, 1951:203; 1955:195. Poynton, 1977:39.

Records. Boma Ulanga (BM), Kilwa (MCZ), Kitaya (MCZ), Kivukoni (BM), Lindi District (MCZ), Luhombero Kilombero confluence (BM), Mahenge (BM), Mikindani (MCZ), Morogoro (BM). Liwale (Loveridge, 1955).

FAMILY HYPEROLIIDAE

Genus *Leptopelis*

Leptopelis Günther, 1859 "1858."

Leptopelis flavomaculatus (Günther)

Hyperolius flavomaculatus Günther, 1864:310.
Leptopelis flavomaculatus (Günther). Poynton, 1977:39.

Records. Mahenge (BM), Msolwa River (BM), Ruvuma (Rovuma) Bay (BM).

Leptopelis argenteus (Pfeffer)

Hylambates argenteus Pfeffer, 1892.
Leptopelis concolor, not Ahl, 1929. Loveridge, 1942:390.
Leptopelis argenteus (Pfeffer). Loveridge, 1951:203.

Records. Mikindani (MCZ), Ruponda (MCZ). Lindi (Schiøtz, 1975).

Discussion. The two Mikindani specimens collected by Loveridge still have tails and are badly desiccated. They do however appear to be *argenteus*. Schiøtz (1975) used trinomials for *argenteus*, considering *concolor* Ahl to be subspecifically related on account of similar morphology, call, and habitat preference. No sign of intergrading was found, however. In view of the exceptional taxonomic difficulties encountered in *Leptopelis*, emphasized by Poynton and Broadley (1987), it is considered inadvisable to use the subspecific category in the genus unless problems caused by intergrading make its use unavoidable.

Genus *Kassina*

Kassina Girard, 1853.

Kassina maculata (Duméril)

Hylambates maculatus Duméril, 1853. Loveridge, 1942:394; 1951:203.

Records. Kitaya (MCZ), Liwale (MCZ), Ruvuma (Rovuma) Bay (BM).

Kassina senegalensis (Duméril and Bibron)

Cystignathus senegalensis Duméril and Bibron, 1841.
Kassina senegalensis (Duméril and Bibron). Loveridge, 1942:395; 1951:203. Poynton, 1977:39.

Records. Kitaya (MCZ), Kivukoni (BM), Lindi District (MCZ), Mahenge (BM), Mbalu River (BM).

Discussion. Of the material examined, only BM 1969.1475 and 1476 from Mbalu River have unbroken stripes of the "*argyreivittis* pattern" (Poynton and Broadley, 1987). Other material examined has the broken "Form 3 pattern" (Schiøtz, 1975) on one or both sides of the body. The Mahenge and Lindi District material has however been mislaid or discarded.

Genus *Afrixalus*

Afrixalus Laurent, 1944.

Afrixalus brachycnemis (Boulenger)

Megalixalus brachycnemis Boulenger, 1896.
Afrixalus p. pygmaeus, not Ahl, 1931. Schiøtz, 1975: 87. Poynton, 1977:39 (part: Mahenge).
Afrixalus brachycnemis (Boulenger). Poynton and Broadley, 1987:187.
?*Afrixalus septentrionalis morerei* Dubois, 1985.

Record. Mahenge (BM).

Discussion. As noted in Poynton and Broadley (1987), the small-sized forms of *Afrixalus* do not have constantly defined diagnostic characters, and their taxonomic treatment has been subject to confusion. According to the criteria adopted by Poynton and Broadley (1987), BM 1969.1280 from Mahenge clearly shows the characters to be expected of a male *brachycnemis*. This is not true of a smaller male, 1969.1279 from the same locality, but it is assumed to be the same species.

A. septentrionalis morerei is a replacement name of *A. pygmaeus* (Ahl) (Dubois, 1985). Schiøtz (1974, 1975) applied the name *A. pygmaeus* Ahl with uncertainty to a form which Poynton and Broadley (1987) believed corresponded with the syntypes of *brachycnemis*. The holotype of *pygmaeus* Ahl has not been directly compared with the *brachycnemis* syntypes, but if it is confirmed that *pygmaeus* Ahl and *pygmaeus* Schiøtz are conspecific, and also synomyms of *brachycnemis* Boulenger, then *septentrionalis morerei* would belong to the same synonymy.

Afrixalus species

Megalixalus brachycnemis, not Boulenger, 1896. Loveridge, 1951:203.
Afrixalus brachycnemis, not Boulenger, 1896. Schiøtz, 1975:84.
Afrixalus sp. Poynton and Broadley, 1987:189.

Records. Liwale District (MCZ), Ruaha River (BM), Sonjo (BM).

Discussion. The single females from Liwale District and from Ruaha River, and the immature specimen from Sonjo, do not present the features necessary for confident diagnosis.

Afrixalus crotalus Pickersgill

Megalixalus brachycnemis, Loveridge, 1942:398.
Afrixalus crotalus Pickersgill, 1984.

Records. Kitaya (MCZ), Mikindani (MCZ).

Afrixalus wittei (Laurent)

Megalixalus wittei Laurent, 1941.
Afrixalus wittei (Laurent). Poynton, 1977:39.

Record. Mbega (BM).

Discussion. In this specimen, the right paravertebral dark band fails to meet its opposite anteriorly on the head, and a fine median dark line runs from the tip of the snout to the tip of the urostyle. More material is needed to determine whether the anterior pattern signifies any intergrading with *A. quadrivittatus* (Werner), discussed by Schiøtz (1975).

Afrixalus fornasinii (Bianconi)

Euchnemis fornasinii Bianconi, 1850.
Megalixalus f. fornasinii (Bianconi). Loveridge, 1942: 395; 1951:203.
Afrixalus f. fornasinii (Bianconi). Loveridge, 1955: 195. Poynton, 1977:39.

Records. Kilwa (MCZ), Kisaye (BM), Kitaya (MCZ), Kugota (BM), Liwale (MCZ), Tunduru (MCZ).

Discussion. The BM Kugota specimen has no dorsal markings, a condition described by Loveridge (1955) in his Kilwa series, and discussed by Schiøtz (1975)

Genus *Hyperolius*

Hyperolius Rapp, 1842.

Hyperolius tuberilinguis Smith

Hyperolius tuberilinguis Smith, 1849. Poynton, 1977: 39.
Hyperolius citrinus citrinus, not Günther, 1864. Loveridge, 1942:407.
Hyperolius concolor tuberilinguis Smith. Loveridge, 1955:195.

Records. Ifakara (BM), Kisanga (BM), Kitaya (MCZ), Mahenge (BM), Mikindani (MCZ), Tunduru (MCZ).

Hyperolius pictus Ahl

Hyperolius pictus Ahl, 1931. Poynton, 1977:39.

Record. Kihanzi/Kilombero (BM).

Discussion. The single specimen from this locality is placed in the highly variable *pictus* with some uncertainty. Confirmatory material is desirable, since the altitude of ca. 240 m is low for this more typically upland species.

Hyperolius quinquevittatus quinquevittatus Bocage

Hyperolius quinquevittatus Bocage, 1866.
Hyperolius puncticulatus subsp. Loveridge, 1955:196.

Record. Tunduru (MCZ).

Discussion. This 27.2 mm female is hardly mistakable. It extends the known range of this form eastwards.

Hyperolius argus Peters

Hyperolius argus Peters, 1854.
Hyperolius ahli Loveridge, 1936. Loveridge, 1942: 404.

Record. Kitaya (MCZ).

Hyperolius puncticulatus (Pfeffer)

Rappia puncticulata Pfeffer, 1893.
Hyperolius puncticulatus (Pfeffer). Poynton, 1977: 39.

Records. Boma Ulanga (BM), Mahenge (BM).

Hyperolius mitchelli Loveridge

Hyperolius mitchelli Loveridge, 1953. Poynton, 1977: 39.

Record. Mahenge (BM).

Discussion. According to Rees's field notes, the *mitchelli* series was collected in January 1963; the *puncticulatus* material was collected in various months, but not between December and February.

Hyperolius pusillus (Cope)

Crumenifera pusilla Cope, 1862.
Hyperolius pusillus (Cope). Loveridge, 1942:412.

Record. Kitaya (MCZ).

Hyperolius nasutus Günther

Hyperolius nasutus Günther, 1864. Loveridge, 1942: 411. Poynton, 1977:39.

Records. Ilonga (BM), Kitaya (MCZ), Kipera (BM), Luheya (BM), Mahenge (BM), Msita (BM).

Discussion. Loveridge's Kitaya material, as currently preserved, is not nasute. However, a reading of Loveridge's comments (1942:411) makes it difficult to assign the material to anything but *nasutus*.

Hyperolius parkeri Loveridge

Hyperolius parkeri Loveridge, 1933.
Hyperolius parkeri rovumae Loveridge, 1942:410; 1955:196.

Records. Kilwa (MCZ), Kisaye (BM), Kitaya (MCZ).

Hyperolius reesi Schiøtz

Hyperolius sp. Poynton, 1977:39.

Hyperolius viridiflavus reesi Schiøtz, 1982:272.

Records. Boma Ulanga (BM), Ifakara (ZMUC), Magombero Forest (ZMUC), Mbega (BM).

Discussion. Specific status for this form is preferred in this paper, in view of reservations or disagreement expressed by Duff-MacKay (1980), Laurent (1983), Poynton (1985) and Poynton and Broadley (1987) regarding Schiøtz's (1975) assignation of many forms, including his *reesi*, to *viridiflavus*. Schiøtz (1982) believed, probably correctly, that *reesi* is most closely related to *H. mariae* Barbour and Loveridge from northeastern Tanzania and southeastern Kenya, but his placing of *mariae* as a subspecies of *viridiflavus* can again be viewed with doubt. Schiøtz (1975) himself noted many pecularities shown by *mariae*, and thought it "tempting to regard it as a full species." The relationship between *reesi* and *mariae* might be clarified by investigating the gap between their known ranges.

Hyperolius marmoratus marginatus Peters

Hyperolius marginatus Peters, 1854. Poynton, 1977: 39.

Records. Ilonga (BM), Luwegu (BM).

Discussion. The identification is based on a typically marked young adult from Ilonga. Two juveniles from this locality and two juveniles from Luwegu are assigned with some uncertainty to this form, since the markings are not distinct. It is perhaps noteworthy that this usually common reedfrog has been so poorly collected. The localities appear to be at the northeastern edge of the range of *H. marmoratus* as a whole, and information about population sizes and densities would be valuable.

Hyperolius marmoratus subspecies

Hyperolius undulatus, not Boulenger, 1901. Loveridge, 1942:402.
Hyperolius flavomaculatus, not Günther, 1864. Loveridge, 1942:403.
Hyperolius sp. Loveridge, 1951:203.
Hyperolius viridiflavus ssp. Schiøtz, 1975:215.

Records. Kitaya (MCZ), Liwale District (MCZ).

Discussion. According to the MCZ catalogue, Kitaya and Liwale material was identified as *marmoratus* subspecies by Laurent. The Kitaya material which Loveridge (1942) listed as *flavomaculatus* was assigned by Schiøtz (1975) to *H. viridiflavus*. Reasons for treating marmorate reedfrogs in the southern third of Africa as *marmoratus* rather than *viridiflavus* have been given by Laurent (1983), Poynton (1985) and Poynton and Broadley (1987).

Schiøtz (1975) suggested that the name *citrinus* Günther is available for Kitaya material, should Loveridge (1942) have been correct in interpreting Günther's "Zambezi Expedition" locality for *citrinus* as Ruvuma (Rovuma) Bay, rather than the Zambezi-Shire Basin. Examination of the BM accessions register gives no confirmation of Loveridge's preference for Ruvuma Bay. It appears that only two amphibian species are specifically entered as being from Ruvuma Bay: 64.19.48 (*Kassina maculata*) and 64.19.49 (*Leptopelis flavomaculatus*). *H. citrinus* Günther was tentatively treated as a synomym of *taeniatus* Peters by Poynton (1964a) and Poynton and Broadley (1987). The material listed as *citrinus* by Loveridge (1942: 407) from the Ruvuma (MCZ 25240 through 45, Kitaya) is *tuberilinguis* (Loveridge, 1955:195).

The Liwale material and MCZ 25299 from Kitaya are brown-colored juveniles with no clear markings. MCZ 25201 through 204 from Kitaya show adult markings which, although not well preserved, seem most similar to those of *marmoratus nyassae* Ahl, discussed by Poynton and Broadley (1987). But as the markings of this form are indefinite and very variable, particular caution is needed when assigning material to it. Identification of the Kitaya and Liwale material will have to await better knowledge of the marmorate reedfrogs of northern Mozambique and southern Tanzania.

FAMILY ARTHROLEPTIDAE

Genus *Arthroleptis*

Arthroleptis Smith, 1849

Arthroleptis stenodactylus Pfeffer

Arthroleptis stenodactylus Pfeffer, 1893. Poynton, 1977:39.
Arthroleptis stenodactylus loennbergi Nieden, 1915. Loveridge, 1942:430.

Records. Boma Ulanga (BM), Kitaya (MCZ), Kitikale (BM), Liage (BM), Lindi (MCZ), Mahenge (BM), Masasi District (MCZ), Mbanja (MCZ), Mikindani (MCZ), Mwaya (BM), Nchingidi (MCZ). Liwale (Loveridge, 1955).

Arthroleptis xenodactyloides Hewitt

Arthroleptis xenodactyloides Hewitt, 1933. Poynton, 1977:39.
Arthroleptis xenodactylus, not Boulenger, 1901. Loveridge, 1942:426.

Records. Mahenge (BM), Mikindani (MCZ), Nchingidi (MCZ).

FAMILY HEMISOTIDAE

Genus *Hemisus*

Hemisus Günther, 1859 "1858."

Hemisus marmoratus marmoratus (Peters)

Engystoma marmoratum Peters, 1854.
Hemisus marmoratum marmoratum (Peters). Loveridge, 1942:432, 1951:204, 1955:197. Poynton, 1977:39.

Records. Boma Ulanga (BM), Ilonga (BM), Kitaya (MCZ), Kivukoni (BM), Lindi (MCZ), Liwale (MCZ), Luhombero (BM), Mikindani (MCZ), Mlahi (BM).

FAMILY PIPIDAE

Genus *Xenopus*

Xenopus Wagler, 1827.

Xenopus muelleri (Peters)

Dactylethra muelleri Peters, 1844.
Xenopus muelleri (Peters). Poynton, 1977:39.

Records. Boma Ulanga (BM), Gunguli (BM), Kivukoni (BM).

ZOOGEOGRAPHY

Southeastern Tanzania falls within the range of what has been termed an East African lowland amphibian fauna (Poynton, 1962, 1990; Schiøtz, 1976). The latitudinal range covered by this fauna is enormous, the most widespread species extending a distance of over three thousand kilometers from Somalia to South Africa. Of the 47 species listed in this paper, 29 (62%) have a range of at least 2,000 km along the lowlands: *Bufo gutturalis*, *B. maculatus*, *Breviceps mossambicus*, *Phrynomerus bifasciatus*, *Pyxicephalus adspersus*, *Hylarana galamensis*, *Hildebrandtia ornata*, *Ptychadena oxyrhynchus*, *P. anchietae*, *P. mascareniensis*, *P. mossambica*, *Phrynobatrachus acridoides*, *P. mababiensis*, *Chiromantis xerampelina*, *Leptopelis flavomaculatus*, *Kassina maculata*, *K. senegalensis*, *Afrixalus fornasinii*, *Hyperolius tuberilinguis*, *H. argus*, *H. mitchelli*, *H. pusillus*, *H. nasutus*, *H. parkeri*, *H. marmoratus*, *Arthroleptis stenodactylus*, *A. xenodactyloides*, *Hemisus marmoratus*, and *Xenopus muelleri*. *Afrixalus crotalus* may prove to be assignable to this group; it has a known coastal range of some 1,300 km (extending southwards to the Beira area), but the true range may be underestimated on account of taxonomic confusion regarding northern Tanzanian material. The species may turn out to have a typical East African lowland range.

In contrast, *Stephopaedes loveridgei*, *Bufo reesi*, *Spelaeophryne methneri*, and *Hyperolius reesi* are known only from southern Tanzania, although the very poor state of collecting in northern Mozambique allows nothing to be said about their limitation southwards. This is also true of *Leptopelis argenteus*, currently known only from Tanzania (Poynton and Broadley, 1987). *Mertensophryne micranotis*, known to occur northwards into Kenya (Grandison and Ashe, 1983), may also extend into northern Mozambique, as does *Bufo lindneri* (Clarke, 1989).

Two treefrogs listed in this paper belong to what Schiøtz (1976) has described as a more western group, with ranges extending across central Africa south of the Congo forest block and its extension into southwestern Kenya. These are *Afrixalus wittei* and *Hyperolius q. quinquevittatus*. Likewise, the wide-ranging *Schismaderma carens*, *Rana angolensis*, *Ptychadena taenioscelis*, and *Phrynobatrachus natalensis* tend to avoid the extreme eastern lowlands, and could be included in a group centered in the interior of the continent (Poynton and Broadley, 1991). Less widespread, but with ranges centered west of southeastern Tanzania, are *Afrixalus brachycnemis*, *Afrixalus* sp., *Hyperolius pictus*, *Hyperolius marmoratus marginatus*, and also *Hyperolius puncticulatus*, although according to current taxonomy, this latter species reaches the coast in northern Tanzania, as discussed in Poynton and Broadley (1987).

The *Hyperolius marmoratus* subspecies from Kitaya and Liwale District cannot receive zoogeographical treatment on account of taxonomic uncertainty and paucity of records. The meagre two records of *H. marmoratus marginatus* allow little to be said about the distribution of the *marmoratus* group as a whole in southeastern Tanzania; but the available records suggest that *H. marmoratus* reaches its northern limit in the area around 8°30′S, in the Luwegu Basin. The southernmost record of *Hyperolius reesi* is at about the same latitude in the Kilombero Basin; if this species is affiliated to the *H. viridiflavus* group, the record indicates the southern limit of the group as a whole. The possibility of sympatry between the *marmoratus* and *viridiflavus* groups could be investigated around the junction of the Kilombero and Luwegu Rivers.

The presence in southeastern Tanzania of the northern *H. viridiflavus* and the southern *H. marmoratus* groups serves to emphasize the zoogeographical richness of the area, as does the presence of the Kenyan–Tanzanian *Mertensophryne* and Tanzanian–Mozambican–Zimbabwean *Stephopaedes*. This richness has tended to be undervalued, perhaps largely on account of the attractiveness of the Afromontane areas of Tanzania.

As "southeastern Tanzania" is taken in this paper to be an area below the 1,000 m contour, the Afromontane Region as described by White (1978) is excluded from it. Species which, according to White's treatment, would be classified as "marginal intruders" from the Afromontane Region could be expected to occur in more elevated areas of southeastern Tanzania, notably the widespread *Strongylopus fasciatus* (Poynton, 1964b), but the only record of a species which can be considered essentially "Afromontane" is the somewhat uncertain identification of a specimen of *Hyperolius pictus*.

The gap of some 1,400 km between the known ranges of *Stephopaedes loveridgei* and *S. anotis* is of the same order as the "Malawi interval" noted by White (1978) to occur in the distribution of several kinds of Afromontane plants. The known range of *S. loveridgei* does however lie below the Afromontane Region as defined by White, as does the range of *S. anotis:* the Chirinda Forest of Zimbabwe in which *anotis* occurs, lying between 1,076 and 1,250 m, is considered by White (1978:484) to be "transitional between Afromontane and lowland forest." Populations of *S. loveridgei* and of *Mertensophryne micranotis* may be considered to inhabit relicts of a formerly more widespread and continuous East African lowland forest, generally believed (e.g., Hamilton, 1976; Coetzee and van Zinderen Bakker, 1989) to have occurred in eastern Tanzania and Kenya during both glacial and optimal interglacial times. The lowland forest contributing to the more southern Chirinda and Dombe Forests is generally considered to belong to the same phytochorion as the East African lowland forest, but an interruption in this phytochorion is usually thought to occur north of the Zambezi Delta (Werger, 1978), which may offer a starting point in

accounting for the apparent vicariation within *Stephopaedes*.

Occupying the same area and habitat as both species of *Stephopaedes* are *Leptopelis flavomaculatus* and *Arthroleptis xenodactyloides* (Poynton and Broadley, 1985a, 1987), but both these species have much more extensive ranges, which include Malawi. More information is needed about the ecology of *Stephopaedes*, in particular the selection of breeding sites, before the relatively restricted ranges of its two species can be accounted for; but, as with *Mertensophryne*, available evidence indicates a particularly close dependence on a strictly forest environment. *Leptopelis flavomaculatus* may prove to be less dependent on a forest environment, while *Arthroleptis xenodactyloides*, which occurs in open country in upland areas, is certainly less so (Poynton and Broadley, 1985a, 1991).

Although southeastern Tanzania has been less intensively collected than some other areas of the territory, notably Afromontane areas, an examination of species lists from surrounding areas suggests only few species that might have escaped sampling. The most obvious is *Ptychadena schillukorum* (Werner), a "secretive species, easily overlooked" (Stevens, 1974), discussed recently by Perret (1987). This species is known from Mozambique–Malawi to the Sudan. Two other species of *Ptychadena*, which belong to the widespread, more western group, could possibly occur in the area: *P. uzungwensis* (Loveridge) and (more likely) *P. guibei* Laurent. The absence of *Tomopterna* species is notable, but the area may be too moist to favor their occurrence. This could also be true of *Bufo garmani* Meek, which has a patchy distribution in East Africa; it could perhaps also be true of dwarf *Bufo* species, such as *B. taitanus* Peters. These species are however easily overlooked (Clarke, 1989), and should be searched for. The moist conditions should favor apodans, but no apodan species have so far been reported from the area. These amphibians are again easily overlooked, and should be searched for. As was noted in the introduction to this paper, the area includes the Selous Game Reserve, and it is hoped that the present study will stimulate further work on the amphibians of this relatively neglected part of Africa.

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GAZETTEER

Boma Ulanga	8 10 S 36 57 E
Gawiro	8 34 S 35 50 E
Gunguli	8 35 S 37 15 E
Ifakara	8 09 S 36 41 E
Ikulia	8 45 S 37 05 E
Ilonga	9 04 S 36 51 E
Kihanzi-Kilombero confluence	8 25 S 36 22 E
Kilwa (Kivinje)	8 45 S 39 24 E
Kitaya	10 40 S 40 11 E
Kipera	8 25 S 36 25 E
Kisanga	8 25 S 36 25 E
Kitikale	7 32 S 37 02 E
Kivukoni	8 11 S 36 42 E
Kiwengoma Forest Reserve	ca. 8 20 S 38 56 E
Kugota	7 51 S 38 25 E
Liage	8 18 S 37 05 E
Lindi	10 00 S 39 41 E
Liwale	9 46 S 37 56 E
Luheya	9 00 S 37 00 E
Luhombero-Kilombero confluence	8 25 S 37 12 E
Lukandi	8 48 S 36 50 E
Luwegu River	8 45 S 37 23 E
Magombero Forest	7 50 S 36 58 E
Mahenge	8 41 S 36 43 E
Maji ya Moto	7 40 S 37 30 E
Masasi	10 43 S 38 41 E
Matumbi	9 29 S 35 31 E
Mbanja	9 24 S 39 45 E
Mbalu River	8 40 S 36 55 E
Mbega	8 38 S 36 08 E
Merera	8 33 S 36 02 E
Mikindani	10 17 S 40 07 E
Mkomangasha	8 58 S 37 24 E
Mlahi	8 30 S 37 12 E

Msita	8 34 S 35 55 E
Msolwa River	8 02 S 37 00 E
Mtilangondo	8 25 S 37 07 E
Mwaya	8 55 S 36 51 E
Nchingidi	10 08 S 39 12 E
Riva Lumango	7 32 S 37 02 E
Rondo Plateau	ca. 10 08 S 39 12 E
Ruaha River	7 56 S 37 52 E
Ruponda	10 15 S 38 42 E
Ruvuma (Rovuma) Bay	10 26 S 40 29 E
Shuguli	8 32 S 37 23 E
Sonjo	7 50 S 36 52 E
Tunduru	11 07 S 37 21 E
Uga	8 33 S 35 50 E

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NEW FLYING LIZARDS AND PREDICTIVE BIOGEOGRAPHY OF TWO ASIAN ARCHIPELAGOS

JAMES LAZELL[1]

ABSTRACT. Two new flying lizards, genus *Draco*, are described from Sangihe Bank, Far Moluccas, Indonesia, and Batanes Bank, Typhoon Islands, Philippines. General species-group level characters of *Draco* are described and depicted. The two Banks and archipelagos are compared to the Lesser Antilles, strikingly similar in physiography. *Draco* is compared to *Anolis* and similarities in patterns of distribution and evolution are predicted.

INTRODUCTION

We should look for knowledge where we may expect to find it . . . .

Then came all legendary monsters. . ., noisome brutes with horny scales. . ., uncouth primeval things, and winged serpents.

W. Somerset Maugham (1908)

Three remarkably similar tropical archipelagos connect very large oceanic islands to each other or to continental shelves. All support remarkably similar lizards.

In the New World, the Lesser Antilles extend from close to the continental shelf of South America, and the large coastal island of Trinidad, nearly to the Greater Antillean Puerto Rico Bank. The Far Moluccas extend from close to the huge island Bank of Sulawesi (Celebes) nearly to the Greater Philippine Bank and the large island of Mindanao. The Typhoon Islands extend from close to the continental shelf of Eurasia, and the large coastal island of Taiwan, nearly to the Greater Philippine Bank (Fig. 1). All three archipelagos are roughly Y-shaped, or doubled for part of their length. All are of volcanic origin. All have at least some islands on some banks with oceanic limestone at elevations too high to be accounted for merely by Pleistocene interglacials. Thus, in each case, some of their islands and banks probably date from at least the Miocene. The three archipelagos are diagrammed in Figure 2.

Darlington (1957:516–517) first suggested the biogeographic analogy of the Philippines to the Antilles. He had clearly in mind the resemblance of the larger, main Philippine islands to the Greater Antilles. In my analogies to the Lesser Antilles, Mindanao on one hand, Luzon on the other, become the counterparts of Greater Puerto Rico.

The name "Far Moluccas" is herein coined because no name for the group collectively currently exists. Indonesia possesses Miangas and the Kawio, Sangihe, Nenusa, and Talaud island groups, but these names do not conform to banks. The Sarangani Bank is within the Philippines.

There is no prevailing wind in the Far Moluccas. Trades often hold sway, but equatorial westerlies often generate south winds at two to five degrees north latitude. Still air—the doldrums—often overrides any surface wind. The humidity is maximal. As in the Lesser Antilles, clouds tend to lie at about 650 m. These create montane rain forest and moss forest or "elfin woodland" zones. There are no arid areas comparable to the rain

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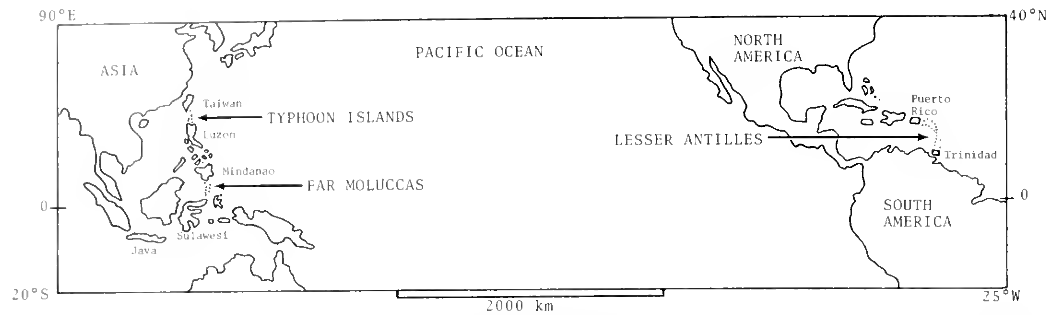


Figure 1. A portion of the world indicating positions of the three compared archipelagos and some other place names mentioned in the text.

shadow zones of the high, montane, cloud-barrier islands in the Lesser Antilles: the near-constant rain and inconstant winds preclude them.

The name "Typhoon Islands" is herein coined as well because no prior name for the whole group exists. Ten of 12 banks are within the Philippines. Five, centrally located, make up the Province of the Batanes. Five, in the South, are collectively called the Babuyans and assigned to Cagayan Province, Luzon. Two banks belong to China. The larger of these, Hungtou Hsu Bank, harbors the large island of Lanyu, or Botel Tobago, or Orchid Island (Ota, 1987); the other is tiny Lu Tao.

The Typhoon Islands lie closely congruent with the principal pathway of the greatest of Earth's cyclonic storms—Pacific typhoons—and span Luzon Strait from the oceanic Philippines to just east of the continental shelf island of Taiwan, China. Much of the warm surface water of the tropical Pacific passes through the Far Moluccas, the Celebes, and Sulu Seas, and forms a huge clockwise gyre in the South China Sea. This water exits again into the Pacific through Luzon Strait. Most of the tropical Pacific's surface water is deflected northward off New Guinea and the Philippines. The present island chain lies where the confluence of these two streams forms *Kuro Siwo*, the Japan (or Black) Current. The Pacific Ocean and South China Sea have different tidal regimes that dramatically affect water movement in Luzon Strait.

To the east of the Typhoon Islands the open Pacific extends some 9,500 km: the greatest fetch of the northeast Trades on Earth. Immediately to the northwest begins the huge Eurasian landmass that generates the seasonal wind patterns called monsoons. These often disrupt or cancel out the strongest Trades. In conflict and concert, these vast forces of wind and water make this island realm the most tempestuous in the tropical world. A concise description of these forces in humanized terms is provided by Gonzales (1966).

All three archipelagos have depauperate highly endemic herpetofaunas in keeping with their oceanic island histories. All have surely garnered their herpetofaunas by over-water "waif" dispersal. The two Asian archipelagos are little-known, but the Lesser Antilles may fairly be said to have provided a disproportionately large share of the data from which biogeographic and ecological theories have been forged.

If the Lesser Antilles today are well-known and well-studied, can we use this knowledge to predict anything of the herpetofaunas of the Far Moluccas and Typhoon Islands? Has biogeography, with its descendent ecological and evolutionary theory, become a predictive science, or is it to remain strictly descriptive, requiring novel sets of postulates

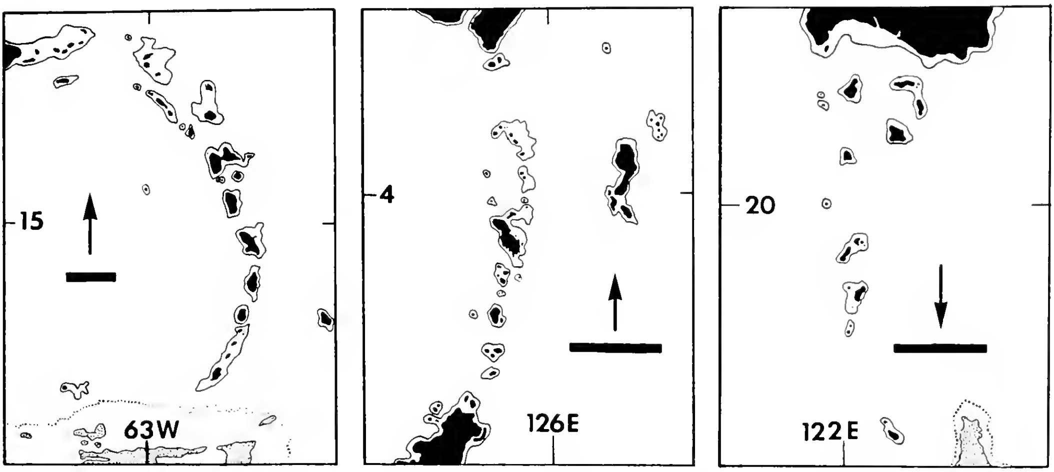


Figure 2. Three archipelagos, left to right: The Lesser Antilles, the Far Moluccas, and the Typhoon Islands. Lines indicate oceanic island banks; the islands are black. Dots indicate continental shelves and lands on them. Bar, in each case, equals 100 km. Longitude east or west of Greenwich is indicated at bottom; a latitude north of the equator is indicated on left. All are shown in mercator projection. Arrows point north. Note the Typhoon Islands are depicted upside-down to enhance comparison.

case by case?

Critical to understanding Lesser Antillean biogeography is the "bank" concept discussed below. Separate banks have at least partially endemic herpetofaunas. Present-day islands on the same bank have weakly differentiated or essentially identical herpetofaunas (Williams, 1969; Lazell, 1972). I shall herein transfer the bank concept, and my notions of its biogeographic relevance, to the Far Moluccas and Typhoon Islands.

My comments on *Anolis* and Lesser Antillean biogeography and physiography are distilled from Lazell (1972). *Anolis* are the most conspicuous and abundant members of the Lesser Antillean herpetofauna. Diurnal, scansorial lizards, they are ornamented with extensible fans and (often) bold patterns and bright colors.

I have made three forays into the Asian archipelagos and found new species of *Draco* each time exactly where predicted. The first new species, *Draco biaro*, has been described (Lazell, 1987a). Two more require description now, and it is time to codify my predictions. Some of the Asian banks and their islands are very difficult of access and a few are dangerous. However, I believe the opportunities for discovery they present are nothing short of wonderful.

Like trunk and big tree *Anolis*, *Draco* are conspicuous, diurnal, scansorial lizards. They are often brightly colored and boldly patterned. Like *Anolis*, they have an extensible, median throat fan or dewlap. In addition, *Draco* have four other fans: a pair of lateral neck lappets and the huge patagia, or wings, supported on thoracic ribs. The patagia are important in courtship and combat displays, as is the throat fan. *Draco* tend to perch high on tree trunks, often head up. They escape by climbing up in a rather graceless, saurian gait. They seem reluctant to enter crowns of trees. They may be selected against doing so by crown-dwelling, lizard-eating snakes.

Draco usually launch and glide when pursued toward tree crowns. I have the impression that they never go down by any method other than gliding, but there are likely exceptions I have not witnessed. It is said by local people that severe storms kill off large numbers of *Draco*. This may limit them on, or exclude them from, small islands.

METHODS

Because I explicitly adopt the view that *Draco* are *Anolis* analogs, I expect the same approaches to study and the same sorts of characters to prove successful in resolving species problems in *Draco*. The first and most fundamental method derives from the exhortation of Williams (1959): these lizards ". . .must be known intimately—anatomically, ecologically, ethologically—. . . if the many puzzles the genus poses are to be solved." This means simply that the animals must be known in life, preferably in the field, under natural conditions. Historically, this view derives from the industry of Samuel Garman in the Lesser Antilles. Barbour (1914) noted: "At first, certain of the so-called conservative zoologists objected at the making of such a large number of new species. Time, however, has justified Garman's work. . ." This view finds an even earlier root in the efforts of Philip Gosse in 1844–46 in Jamaica, as reported by Underwood and Williams (1959).

The clear picture of *Draco* systematics developed by Inger (1983) at Nanga Telakit on Borneo depended on knowledge of the animals in life. Inger could not have derived it from examination of preserved museum specimens alone, but considered coloration, patterns, behavior, and ecology.

The difficulty for systematists is codifying field knowledge of animals as characters that lead the field biologist to recognize and rank taxa and that other systematists can utilize. *Draco* represent a novel challenge because no one has previously considered a number of taxa from distant portions of the generic range in life. I have now come to know *Draco* on Hainan Dao, China, in Indonesia, and in the Philippines. I have examined hundreds of museum specimens in the light of the generic revisions provided by Hennig (1936), Musters (1983), and Inger (1983). It is apparent that some characters thought trenchant and diagnostic at high levels, like number of patagial ribs and presence of a tympanum, vary within some very small demes and are never diagnostic at any level higher than local species. Color characters, virtually unknown to the previous revisors except as patterns retained in alcohol or in life at local sites, are the most useful for distinguishing forms. Extrapolating from *Anolis*, we might expect morphologically similar species, difficult or impossible to distinguish on mensurable or meristic characters, to be quite distinct in colors. That is exactly what Inger (1983) found at Nanga Telakit, Sarawak, Borneo. That is also what Taylor (1922) reported on Mindanao, but recent revisors (including Inger) did not credit his observations (but see Ross and Lazell, 1991).

The coloration and pattern of the patagia are especially critical. I have diagrammed frequently observed patterns and components so as to codify an applicable vocabulary (Fig. 3). Some require further comment.

Costate patterns typically involve enlarged, distinctively colored scales in zones centered along the patagial ribs. Intercostate patterns, just the opposite, involve pigmented skin in the membrane expanses between the ribs.

Reticulated patterns may extend over the entire patagium or be confined to smaller areas on it. For example, one sees reticulated intercostate patterns.

Radials are notable features of most *Draco* patagia. They do not truly radiate from any point, but arise more or less antero-medially and extend, often bifurcating one or more times, postero-distally. It is frequently difficult to determine if the scales in the radials are actually enlarged or merely appear so because they are distinctively colored. Frequently pattern components, sometimes extending from trunk figures onto the proximal patagia, seem to be becoming concentric elements, but fragment into spots or short bars centered along the radials.

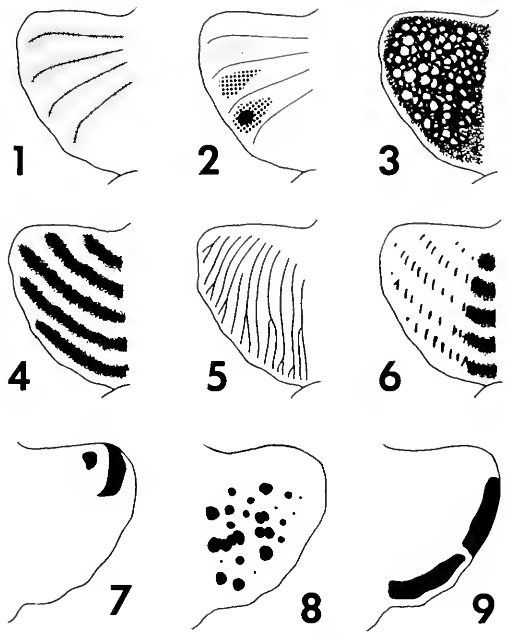


Figure 3. Diagrammatic patagia of *Draco*. Top is anterior. Patterns, in dorsal view, include: 1, costate; 2, intercostate (ocellate posteriorly); and 3, reticulate. Pattern components, in dorsal view, include: 4, concentrics; 5, radials; and 6, concentrics picked up on radials. Pattern components, in ventral view, include: 7, bracket; 8, spots; and 9, marginal (anterior) and submarginal (posterior) zones.

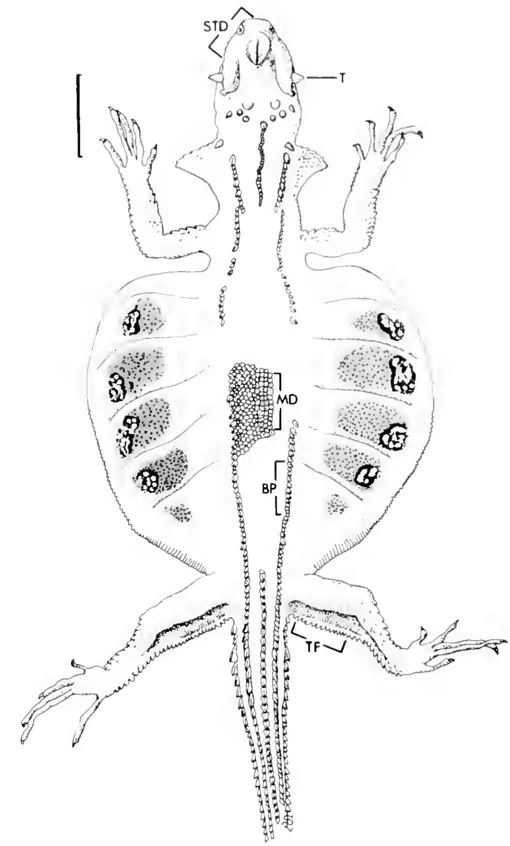


Figure 4. Dorsal view of *Draco everetti* showing measurements, scales, and counts of systematic value. STD, standard distance: tip of snout to center of eye. T, supraciliary thorn. MD, middorsal scales counted in STD. BP, basipatagial scales counted in STD beginning at level of last rib. TF, thigh fringe scales in STD. Bar, upper left, is one cm. (From Ross and Lazell, 1991.)

The ventral patagia are usually quite differently colored and patterned from their own dorsal surfaces. Of course, in front of strong light, the dorsal components may show through the membranes. The reverse is also true, though usually less noticeable. The pattern components I have depicted ventrally in Figure 2 may also occur dorsally. Sometimes ventral elements may underlie and correspond to dorsal elements, and vice versa.

The bracket pattern often encloses other markings or distinctive colors. Brackets may begin at the patagial margin and become submarginal posteriorly. There are often marginal or submarginal spots, bars, or zones along the patagial borders.

I discuss my use of standard distance counts in Ross and Lazell (1991, and references therein). Briefly, these enable scale count and size comparisons from various different areas of the body and therefore seem more useful than longer counts which may confound real differences. Places where I usually make standard distance (STD) counts are shown in Figures 4 and 5. Juveniles are not used in STD counts because of their disproportionately short snouts.

The tails of *Draco* may bear several sorts of scales of disparate sizes, even on the same lizard. These are easily quantified by counting the number of scales on different aspects of the tail contained in the length of the extended lower leg (Fig. 6). Statistical significance of diagnostic scale counts has been

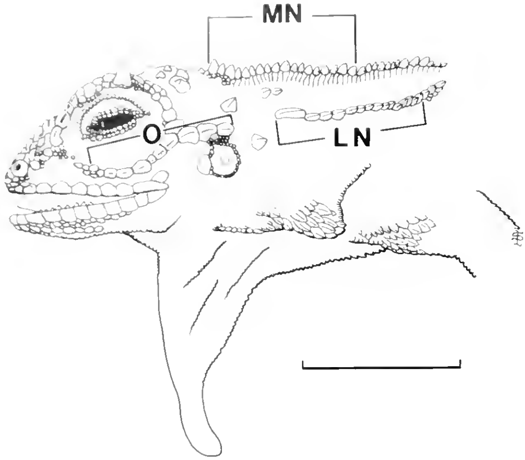


Figure 5. Head of *Draco everetti* showing scale counts made in STD. O, oculotemporals. MN, middorsal nuchal crest scales beginning at first enlarged scale. LN, lateral nuchal crest scales beginning at first enlarged scale and extending for the minimum count of contiguous scales. Bar, lower right, is one cm. (From Ross and Lazell, 1991.)

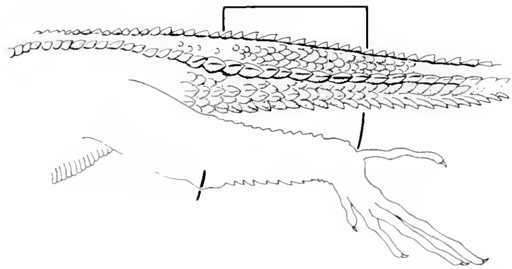


Figure 6. Side view of tail of *Draco everetti* showing method of counting various sorts of caudals and crest scales in the length of the extended lower leg. In this specimen the length of the lower leg is one cm. (From Ross and Lazell, 1991.)

evaluated with student's T test.

Draco, like *Anolis*, often change colors and even patterns. This ability to make physiologically controlled color changes is direct evidence of the great adaptive importance of color to the living lizards (Lazell, 1967). In describing colors I try to use familiar terms and eschew various rigorous standards simply because changes in shade, darkness, or pallor may occur both frequently and rapidly.

My views of evolutionary systematics are derived directly from Simpson (1961) and codified in Lazell (1972, and works cited therein). They would seem to bear some repetition here in light of the chaotic, mutually exclusive, and contradictory systematic views promulgated by various warring factions of biologists today. I seek to classify organisms on the basis of relationship.

Relationship, however, is not a property of organisms. Relationship cannot be measured, weighed, or quantified. Relationship is imponderable and can only be subjectively assessed. I use mensurable and meristic characteristics of organisms in attempting to assess relationship. I use colors too, and often prefer them, giving them great weight. I use indirect evidence about organismal lineages. I use inferences about behavior, ecology, and lineage histories.

I embrace the notion of Darwin (1873): "The periods during which species have undergone modification . . . have probably been short in comparison with the periods during which they retained the same form." Evolutionary rates vary. They vary between lineages at the same time, between lineages at different times, and within lineages at different times. Gould (1982, and works cited therein) has virtually built a career around the celebration of spectacularly different evolutionary rates, quite without acknowledging his debt to Darwin (but see Dawkins, 1987:229–230, 236, and 240–252). My study of island populations and patterns of differentiation beautifully demonstrates to me—albeit indirectly—the reality of different evolutionary rates.

Because I know relationship is imponderable and evolutionary rates are variable, I reject the cladistic notion that relationship is precisely the inverse of lineage age. I know new species have evolved in isolation while older species have retained older parapatric interbreeding subspecies. I am not the least bit troubled by the existence of a relatively young taxon at a higher rank than a relatively old one. Insular patterns of dispersal and evolution necessitate that many species will be-

come "paraphyletic" while spawning other, new species. Some of the latter might evolve into novel genera without notification to the folks back home, so to speak. Evolution in an isolated lineage descended from one member of a pair of closely related lineages need in no way alter the relationship of members of that pair to each other.

Simply put, two parapatric, intergrading subspecies may remain exactly that, while the isolated descendent of one of them proceeds to evolve into a new species somewhere else. I see this phenomenon frequently, for example in the members of the *Anolis cristatellus cristatellus*, *A. c. wileyae*, and *A. ernestwilliamsi* complex in the Antilles (Lazell, 1983).

Believing that evolutionary relationship is precisely equal to the inverse of lineage age makes no sense to me.

Hennig (1936) was appalled at the proliferation of *Draco* species being described from small islands. His references are obscurely cited but fortunately available in Jacobs (1983). Hennig (1936, fig. 7, p. 163) used some color characters, notably deriving concentric patagial groups from attendant trunk markings. I do not find this method particularly useful because patagial markings may be quite independent of trunk pattern. Although he acknowledged the importance of color in species recognition, Hennig proceeded to synonymize many quite distinctively patterned, widely isolated forms.

My view of insular forms is in essence diametrically opposed to Hennig's. I am wholly convinced, by the arguments of Mayr (1940, and numerous since), that geographic isolation results in speciation. The second law of thermodynamics precludes isolated populations from remaining genetically similar. Even in the absence of strong selection pressures, the complex processes of molecular replication guarantee entropic, divergent drift. As long ago elucidated by C. C. Li (1955) and others, genetic differences are simply never neutral in the face of selection. At the very least, numerical advantage results in ultimate populational sweep. In fact, selection pressures on the colonists of oceanic islands are normally great and disparate.

The processes of overwater waif dispersal and irregular colonization – some of those biological and historical factors celebrated by Lack (1976) – necessitate different islands operating as very distinct evolutionary theaters. When a group of forms presents a pattern of regular, progressive change in an archipelago, it may be appropriate to regard those forms as expressing geographic variation in one species (Wright, 1941, 1943; Lazell, 1964a, 1964b; Gould and Paull, 1977).

Quite opposite situations may obtain. For example, geographically proximate forms may be more different from each other than one or the other is from a more distant population (Gould and Paull, 1977:20–21). This may be interpreted as classic character divergence resulting from failed invasions and, therefore, as clear proof of full species level (Williams, 1969; Lazell, 1972:103–104; Goodyear and Lazell, 1986).

I will classify absolutely distinct, geographically isolated (dichopatric) forms as full species unless I see indicative evidence that they fit into a larger pattern of geographic variation in a more widespread species (Lazell, 1972:15–16).

THE FAR MOLUCCAS
Figure 7

There are 16 banks between Sulawesi and Mindanao. In addition, the Nain Bank lies just off the northwest side of the tip of the Minahasa Peninsula. I visited Nain and Mantehage, the largest islands on this Bank, in 1986. People there knew flying lizards, *chichak terbang*, but I could secure no specimens. In light of what I now know about the

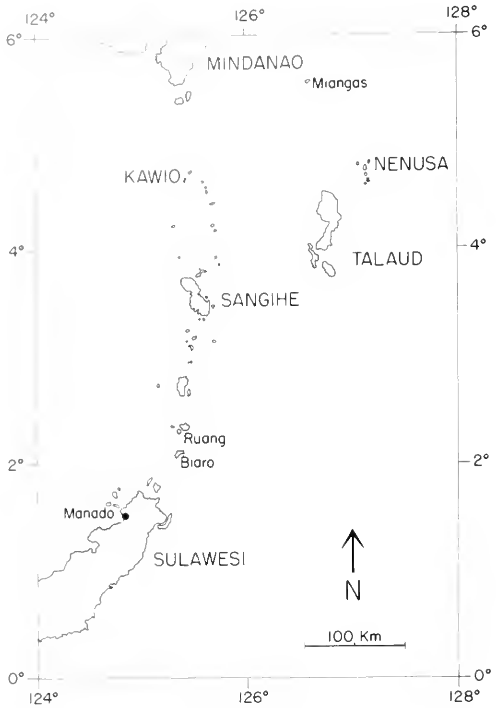


Figure 7. The Far Moluccas, between Mindanao, Philippines, and Sulawesi, Indonesia. Bank edges, at the approximate sea level during a glacial maximum, ca. 100 m below present, are dotted. (Modified from Lazell, 1987b.)

local apparent absence of *Draco* in some areas, I believe Nain Bank should be revisited.

At the present time it is reportedly unsafe for Americans (or other foreigners) to attempt going to the Sarangani Bank, Philippines. Some of the Indonesian islands, like Miangas and the remote Kawios, are hard to locate from the open sea in a small boat. Some of these small islets may lack *Draco* (as Aves and Saba lack comparable *Anolis* species in the Lesser Antilles). I note that Miangas, however, looks analogous to Sombrero, and that remote cay supports a generalized trunk perching *Anolis* (with no trunks to perch on). Miangas certainly supports palm trees, for Magellan called it "Palmas" (Morrison, 1974).

After a two-year absence, I returned to the Far Moluccas in March, 1988. Despite inclement weather, 37 specimens of a strikingly distinctive new *Draco* were collected on Sangihe.

Draco caerulhians sp. nov.

Type. MCZ 173321, Fentje Kodong coll., 20 March 1988 (Fig. 8).

Type-locality. Manganitu, Sangihe, Indonesia. See Figure 9.

Diagnosis. A small *Draco* (males to 74 mm, females to 82 mm, SVL) with five ribs in the patagium and a well-developed tympanum. Scales small: 14–18 (av. 16 ± 1.2) middorsals and 12–18 (av. 15 ± 1.5) midventrals in STD; 20–25 (av. 22 ± 1.6) paired dorsal caudals in length of extended lower leg; 8–12 (av. 10 ± 1.1) postrostrals. No lateral nuchal, basipatagial, or caudal crests; no spike-like or thorn scales. Patagia concentrically patterned; male dorsal patagia of somber brown and dark gray-brown marbling; female dorsal patagia of rich ochre-yellow to orange-brown and contrasting dark gray-brown marbling. Male throat fan and ventral lappets yellow.

Description of the Type. MCZ 173321 is an adult male 72 mm SVL, with a 129 mm tail (179% of SVL). STD is 7.9 mm, 11% of SVL. Twelve scales border the rostral posteriorly. There are 16 smooth middorsals, 15 keeled midventrals, and 18 oculotemporals in STD. The midnuchal crest consists of six blade-like scales anteriorly declining to tectiform scales rapidly; it is not especially prominent. There is no lateral nuchal crest, but a few scales in a small patch about one STD posterior to the orbit are enlarged; the biggest is blunt and not higher than long. There are no enlarged basipatagials.

There is no caudal crest. The middorsal caudals are the largest, paired, and keeled. There are 23 in the length of the extended lower leg.

The throat fan is bluntly hooked, about 17% of SVL, and about 90% of head length.

The adpressed hindlimb just reaches the

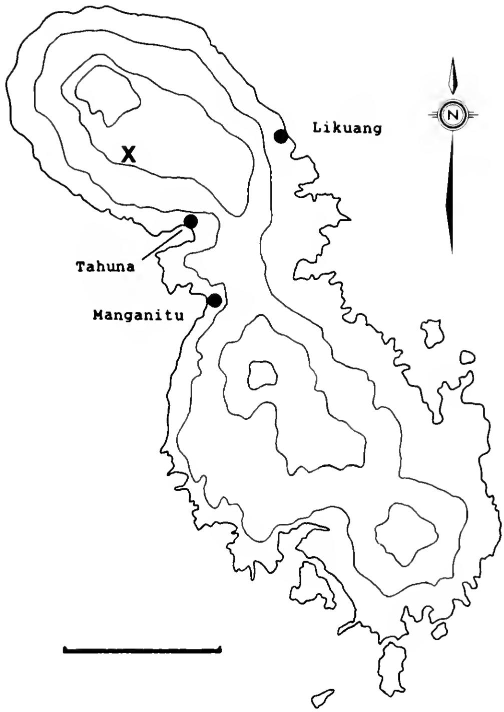


Figure 9. Sangihe, Far Moluccas. Contours approximate 200, 500, and 1,000 m but are drawn from a Bartholomew map of scale 1:5,000,000, and thus are not accurate. Localities where *Draco caerulhians* was collected are named and dotted. X marks the spot for RMNH 24252. Bar, lower left, is 10 km.

axilla. The nasal turrets are oriented dorsolaterally. There are five ribs in the patagium.

Coloration in life was gray-brown with a boldly contrasting head and neck pattern but somber patagia. Dorsal nape and midnuchal crest were marked with sooty black set off by tan-white. The light color shaded to ochre-yellow lateral nape spots, facial spots, and marbling. The chin was blue-gray with yellow spots. The blue-gray extended onto the base of the throat fan where it blended with yellow to produce green tones and dissipated distally into gray streaks. The throat fan was predominantly bright lemon yellow.

The lappets were dark gray-brown spotted with ochre dorsally, and rich, deep yellow ventrally, edged with dark blue-gray.

The chest was bright yellow shading to cream-gray on the abdomen. The underside of the tail was ash-gray and contrasted with the abdominal color.

The dorsal patagia were chocolate brown with about 15 ashgray radials broken by five concentric bands of sooty marbling. The ventral patagia were pale blue-gray with soot-black margins and two irregular sooty blotches roughly corresponding to dark dorsal concentrics.

Color change was dramatic but affected the head and trunk, not the fan or patagia. In the lightest, at-rest condition, described above, the dorsal pattern consisted of forward-pointing gray V shapes set off by lighter gray-brown. In the dark, disturbed condition, the pale tan-white of the nape became rich fawn-brown and the dorsal pattern emerged as sooty diamonds.

When caught, this individual gaped, displaying spectacular, brilliant blue gums and inside lower lip. Blue extended over the roof of the mouth. The upper lip was bright, opaque white. The tongue was rather translucent flesh-pink with a smoky-gray tip.

Male Paratypes. A total of 21 collected at Manganitu by F. Kodong, J. Rimbing, R. Tahulending, and J. Lazell on 20 March 1988: MCZ 173319, 173323, 173325, 173327, 173329, 173331, 173334–50. One of these, MCZ 173342, 73 mm SVL, has been donated to the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH, #25764) after examination.

Adult males measured 55 to 74 mm, average 64 mm, SVL. Seemingly complete tails are 177–185% (av. 181%) of SVL. STD is 11–12% of SVL in all adults. Two juveniles, MCZ 173339–40, both 48 mm SVL, have disproportionately short snouts.

Squamation is similar to that of the type. There are 8–12 (av. 10) scales bordering the rostral posteriorly. There are 14–18 (av. 16) smooth middorsals and 14–18 (av. 16) keeled midventrals in STD. In all, the oculotemporals are weakly differentiated from the

other head scales; there are 15–20 (av. 18) in STD. In all, the midnuchal crest begins as a few blade-like scales and diminishes rapidly to low, tectiform scales.

In all, there are from one to a few enlarged scales on the lateral nape about one STD posterior to the orbit. The largest of these is rarely higher than long and never forms a prominent spike or thorn.

A few individuals (e.g., MCZ 173327, 173339–40) have one to three slightly enlarged basipatagials, but these do not form a crest.

The caudals are always low and keeled. The middorsal pair are the largest. There are 20–25 (av. 23) in the length of the extended lower leg.

The throat fan is always bluntly hooked and short, 82–91% (av. 88%) of SVL.

The nasal turrets always orient dorsolaterally and there are invariably five ribs in the patagium. The adpressed hindlimb usually reaches the forearm insertion, but may fall a little short of it.

The tympanum is always differentiated, much larger than the surrounding scales, and its diameter is more than 10% of STD.

Coloration in life was basically similar in all males, including the juveniles, MCZ 173339–40. MCZ 173327 had the dullest facial coloring, approaching simple gray and white. MCZ 173331 had the brightest green throat fan tones, green tones where his yellow facial spots blended with the blue-gray ground color, and the brightest yellows. MCZ 173325 was the darkest specimen seen. Even in his lightest extreme he had an ochre chest, bold, dark gray streaks in the bright yellow throat fan, and the chin and head very dark gray spotted with orange-yellow.

The balance of warm brown and darker, sooty-color on the dorsal patagia shifts. Some agreed with the type in having the lighter color predominant and the darker appearing as concentrics upon it. Others, like MCZ 173329, had largely sooty patagia upon which brown appeared as concentrics. The lighter color (brown) corresponds to the dorsal trunk ground color and the darker (sooty) emanates from the V-shaped or diamond dorsal trunk markings.

The ventral patagia vary in amount and intensity of dark marking. Most had the bold, near-black margin described for the type and two to four irregular sooty blotches in a roughly concentric pattern on the pale gray-blue ground color. In several, the dark markings were slate-gray and one, MCZ 173344, had very reduced, slate-gray ventral concentrics.

In all, the throat fans were largely lemon yellow, brightest distally. Some showed little proximal gray streaking (e.g., MCZ 173329). The lappets varied from lemon yellow to deep sulfur-yellow ventrally with blue-gray to sooty borders.

All gaped when caught, showing brilliant blue and white.

Female Paratypes. Eight females were also collected at Manganitu by F. Kodong, J. Rimbing, and J. Lazell, 20 March 1989: MCZ 173320, 173322, 173324, 173326, 173328, 173330, and 173332–3. One of these, MCZ 173328, 70 mm SVL, is now RMNH 25763.

Females average larger than males: 59–82 (av. 73) mm SVL. The difference is statistically significant at the 95% level of confidence. Their tails are 171–181% (av. 178%) of SVL. I could detect little difference in squamation between the sexes. The females had 14–17 (av. 16) middorsals in STD and 12–16 (av. 14) midventrals in STD. The count for midventrals is lower than in males but not significantly different. The oculotemporals are similar, 15–19 (av. 18) in STD. There is a slightly enlarged lateral nape scale, usually smaller than that seen in males. The midnuchal crest is less developed in females; it consists merely of enlarged dorsal granules.

The caudals of females are like those of males, 20–25 (av. 22) in the length of the lower leg. There is no extensible throat fan in females. The loose skin of the throat is gray, usually with lighter and darker tones in longitudinal streaks. The tympanum is always differentiated and its diameter is at least 10% of STD. In two, MCZ 173324 and 173333, the tympanic border is encroached by incomplete sutures from adjacent scales, as in Musters (1983, figure 2b, p. 5).

The nasal turrets and five patagial ribs are as in males.

The adpressed hindlimb usually falls a little short of the forelimb insertion, but may reach it in MCZ 173328 and 173332.

This species is strikingly dichromatic. The females are much more brightly colored and boldly patterned than the males. In life, females averaged lighter, warmer brown than males; their dorsal trunk markings were more elaborate. In the boldest condition, six sets of transverse markings are apparent. The anteriormost is similar to the male's nape pattern but colored in soot-gray and brown. The remainder were roughly diamond-shaped, sooty markings with brown interiors middorsally. The third, on the back of the chest, elaborated to wavy, scalloped bands extending laterally to correspond with a bold upper arm band. The fourth, at midbody, extended onto the patagia (see below), as does the fifth. The sixth is on the tail base. Between the bands, from third to sixth, were bold ash-gray spots. Anterior to the third the spots are irregular and indistinct. Posterior to the sixth the tail was simply banded in shades of brown.

The head and chin were patterned in beige to golden brown and chocolate to gray-brown. The chest was cream-color, usually marked with irregular gray spots or marbling. The belly was near-white and the underside of the tail was a slightly contrasting shade of gray.

Dorsally the patagia were rich ochre-yellow to orange-brown with four to six irregularly concentric zones of sooty to chocolate brown. Or, one may interpret the pattern as dark with light, yellow to orange, concentric zones. The light color was an intensified extension of the dorsal ground color; the dark was elaboration and branching from the dark trunk figures.

Ventrally the patagia appeared largely yellow: usually bright, deep yellow to ochraceous orange. Concentric zones of gray-brown marbling terminated distally in sooty blotches which often amalgamated to form a sooty margin.

Among females, MCZ 173320 had the most brilliant ventral patagia: rich orange-yellow. MCZ 173324 had the dullest, with dark dorsal patagial color showing through to subdue and gray the yellow tones.

The blue and white gape is constant and striking.

A female paratype, MCZ 173322, is depicted in Figure 8.

Additional Specimens. Specimens from two other lowland localities were collected by Kodong and Lazell and one was secured on the flank of the highest peak, Gunung Awu, by Dr. Frank Rozendaal.

Two males and a female from Tahuna, MCZ 173314–6, captured 18 and 19 March 1988, were indistinguishable from most topotypic Manganitu specimens.

A pair, MCZ 173317–8, from Likuang on the opposite, eastern coast, are very similar too, but had the most ovate middorsal figures, less diamond-shaped than is typical. Also, this male, MCZ 173317, was the only one seen without any blue-gray or gray streaking proximally in his lemon-yellow throat fan.

The specimen from Gunung Awu, RMNH 24252, is an adult male 65 mm SVL. Rozendaal (in litt.) reports it was taken on the SSW slope of the mountain at about 500 m. It has the best-developed oculotemporal series seen in this species, only 14 scales contained in

STD. Color photos made of the fresh-dead specimen in May 1985 (dorsal and ventral of whole animal, and side view of head) depict a dark specimen with an olive cast dorsally, the venter and fan pale yellow muted with gray. There were very dark gray streaks—the boldest seen on any specimen—invading the throat fan. The specimen was shot and it is difficult to evaluate how much color change was affected by trauma. The possibility of a distinctive montane population on Sangihe is considerable.

Because geographic variation in this species cannot be evaluated with the limited material before me, I elect to designate only specimens from Manganitu as formal paratypes. While these additional specimens have aided me in forming my view of the species *D. caerulhians*, they might represent one or more different subspecific taxa.

Etymology. The name *caerulhians* is Latin, a noun in apposition, meaning the blue gaper.

Comparisons. Draco caerulhians requires close comparison only to the other small-scaled, crestless, and spikeless forms in the *lineatus-spilonotus* assemblage. This assemblage, however, is vastly more complex than imagined by Hennig (1936), Inger (1983), Musters (1983), or Lazell (1987a). I have been able to examine the types of *spilonotus* (BMNH 1946.8.27.27) and *bimaculatus* (BMNH XXII.1.g.). *D. lineatus* Daudin (1802), from Java, has no type. Hennig (1936:195–196) saw only three Javan specimens. Musters (1983:35) examined these and a fourth. Inger (1983:2) saw no Javan material and based his view of the species on the type of *spilonotus*, 18 more Sulawesi ("Celebes") specimens, and 21 from Amboina. I have never seen *lineatus* and my earlier view of *spilonotus* (Lazell, 1987a:6–7) cannot now be reconciled with fresh material I obtained alive much closer to the type-locality of Manado, Minahasa, Sulawesi: MCZ 173351–5, discussed below and depicted in Figure 8.

Trinomials are, at present, inappropriate: they presuppose relationships unknown and unverified by any biological observations. I have already reverted to the position of Taylor (1922) and Inger (1983) that Philippine *D. bimaculatus* is distinct from *lineatus* or *spilonotus* (Ross and Lazell, 1991). I see none of these as conspecific with *Draco biaro* Lazell (1987a). I must now give *spilonotus* its due because two apparently quite distinct, yet rather similar, forms occur within short distances of Manado, Sulawesi. Only one can be real *spilonotus* and I view the chance of either being conspecific with a Javan, continental shelf form as remote. In any case, *Draco lineatus* is a virtually unknown taxon. Even the Javan specimens seen by Musters (1983:36–37) are "faded" and in "bad condition." In my opinion, redescription of *D. lineatus*, complete with a neotypic designation based on material known and documented in life, should proceed from a study of geographic variation on and around Java, and precede any attempt to ally oceanic island taxa with *lineatus* at species level.

From 24 to 30 March 1988 colleagues and I attempted to locate *Draco* in and around Manado. The closest population we could find was at the foot of Gunung Kalabat, around the village of Airmadidi, ca. 18 km east of Manado.

The four males, MCZ 173351–4, and one female, MCZ 173355, from Airmadidi are immediately distinct from the Batu Putih specimens I collected in 1986 (Lazell, 1987a:6–7) in lacking green. The males have small, blunt throat fans 69–79% (av. 74%) of head length, which is 18–22% (av. 21%) of SVL. Throat fans for the Batu Putih specimens are 96–102% (av. 99%) of head length (Lazell, 1987a). It is about 20 km, straight-line, from Airmadidi to Batu Putih. Both localities are near sea level, but separated by mountains approaching 2,000 m. My experience at Airmadidi on 25 March 1988 pro-

vided a sort of déjà vu, recalling 18 June 1958 on Dominica, Lesser Antilles (Lazell, 1962). All previous authors have agreed that the size and shape of the male throat fan is a trenchant character in *Draco* and I am not inclined to disagree.

The types of *Draco spilonotus* Günther (1872) are both males: BMNH 1946.8.27.26 and 27, the latter designated lectotype by Musters (1983:50). I have examined both. In throat fan size and shape they agree with the Airmadidi series, not those from Batu Putih (fan is figured by Hennig, 1936:168). Apart from the lack of green coloration, so striking at Batu Putih, the Airmadidi specimens closely resemble the Batu Putih series described (Lazell, 1987a) in pattern and patagial coloration. Like the Batu Putih males, Airmadidi males may have bright salmon-red (MCZ 173354), orange (MCZ 173352), or brilliant yellow (MCZ 173351, 173353) patagia.

The pattern of the lectotype of *spilonotus*, BMNH 1946.8.27.27, is beautifully preserved; the patagia are now pale yellow. This specimen was a nearly precise match in coloration and pattern for MCZ 173353 on 6 November 1989, at which time the Airmadidi MCZ specimen had been in fluid more than 18 months. Structurally, the lectotype differs from the Airmadidi series in many characters. I give the measurements and counts of BMNH 1946.8.27.27 followed by those of Airmadidi males, MCZ 173351–4.

The SVL is 60.5 (49–64, av. 59). The STD is 11% of SVL (12–13, av. 12). The throat fan is 71% of head length (69–79, av. 74) and 15% of SVL (18–22, av. 21). The tympanum is well developed and 17% of STD (present only in two, where only seven and nine percent). There are 11 postrostrals (8–10, av. 9). There are 13 middorsals in STD (14–15, av. 14) and 13 midventrals (14–15, av 14). There are 26 lamellae under the fourth toe (25–27, av. 26).

There are 18 pairs of midcaudals in extended lower leg (16–18, av. 17 ± 0.7). These relatively large midcaudals provide the quickest quantitative distinction between Sangihe *caerulhians* and Sulawesi *spilonotus*.

Perhaps notably, the oculotemporals of the lectotype of *spilonotus* are large; there are only 12 in STD (14–20, av. 16).

The paralectotype, BMNH 1946.8.27.26, is a male 58 mm SVL. The throat fan, 11 mm, is 91% of head length and 19% of SVL. There are 18 midcaudals in the length of the lower leg. There is an enlarged tympanic scale 14% of STD. In all other respects except middorsals in STD this specimen agrees with the Airmadidi series. With only 13 middorsals in STD, however, it agrees with BMNH 1946.8.27.27, the lectotype. The color pattern is well preserved and agrees with the other Minahasa males. The patagia are pale yellow with a little dark spotting proximally in concentric bands.

The most proximate geographic relative of *Draco caerulhians* is *D. biaro*, from the isle of Biaro ca. 150 km and six banks to the south. The two are immediately distinct in coloration and pattern but very similar in squamation. A well-developed tympanum is always present in *D. caerulhians*, and always has a maximum diameter greater than 10% of STD. More than 90% of *D. biaro* have the tympanic area clothed in small, granular scales. In one *D. biaro*, a juvenile MCZ 170919, sutures enter the tympanic region partially partitioning the thin skin there; perhaps with age these would have developed into an arrangement of small scales as the tympanic skin thickened. In any case, the condition is not like that seen in *D. caerulhians*.

Only one available *D. biaro*, MCZ 170899, has an enlarged tympanic scale approximating that of *D. caerulhians*. In this individual the enlarged scale is only 8.8% of STD.

In all adult *D. biaro* there is an enlarged, thorn or blade-like lateral nuchal scale within

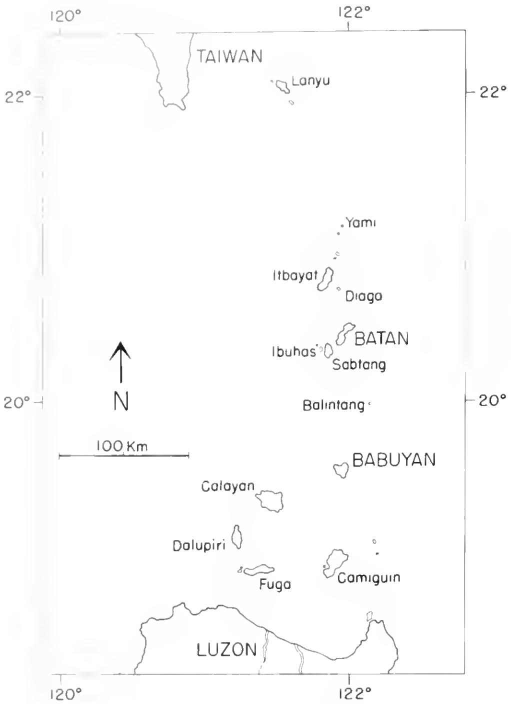


Figure 10. The Typhoon Islands, between Taiwan, China, and Luzon, Philippines. Continental shelf and Bank edges, at the approximate sea level during a glacial maximum, ca. 100 m below present, are dotted.

a patch of somewhat enlarged scales a little more than one STD posterior to the orbit. This scale is always at least as high as its greatest basal diameter. In *D. caerulhians* the patch is present and one scale is usually notably enlarged, but it does not form a blade or thorn, and is never as high as its greatest diameter.

Sexual dimorphism is strong in *Draco caerulhians* but very weak in *D. biaro*. For example, the enlarged lateral nuchal is most prominent in males of *caerulhians*, very weak in females. It is equally well developed in both sexes of *D. biaro*. More significantly, I believe, the difference in size between the sexes of *D. caerulhians* is significant at the 95% level of confidence: 16 males are 60–74 (av. 69) mm SVL, while 8 females are 68–82 (av. 74) mm SVL.

Males of *D. caerulhians* are drab and somber, like all of those of *D. biaro*, except for their bright yellow fans and ventral lappets. Female *D. caerulhians* are spectacularly distinct with their bold patagial patterns of bright ochre to orange-yellow.

Ecology and Behavior. Inclement weather prevented the sorts of prolonged observations one is often able to make of *Draco*. Nevertheless, those seen alive by me occupied the generalized *Draco* niche: conspicuous, diurnal trunk dwellers seen at rest at 2 to 10 m above the ground. Coconut palms and fruit trees are favorites. Whitten *et al.* (1987) discussed deforestation of Sangihe. While I do not doubt that human omnipresence has vastly modified Sangihe's vegetation, the island today is covered with large trees. Most of it seems good *Draco* habitat.

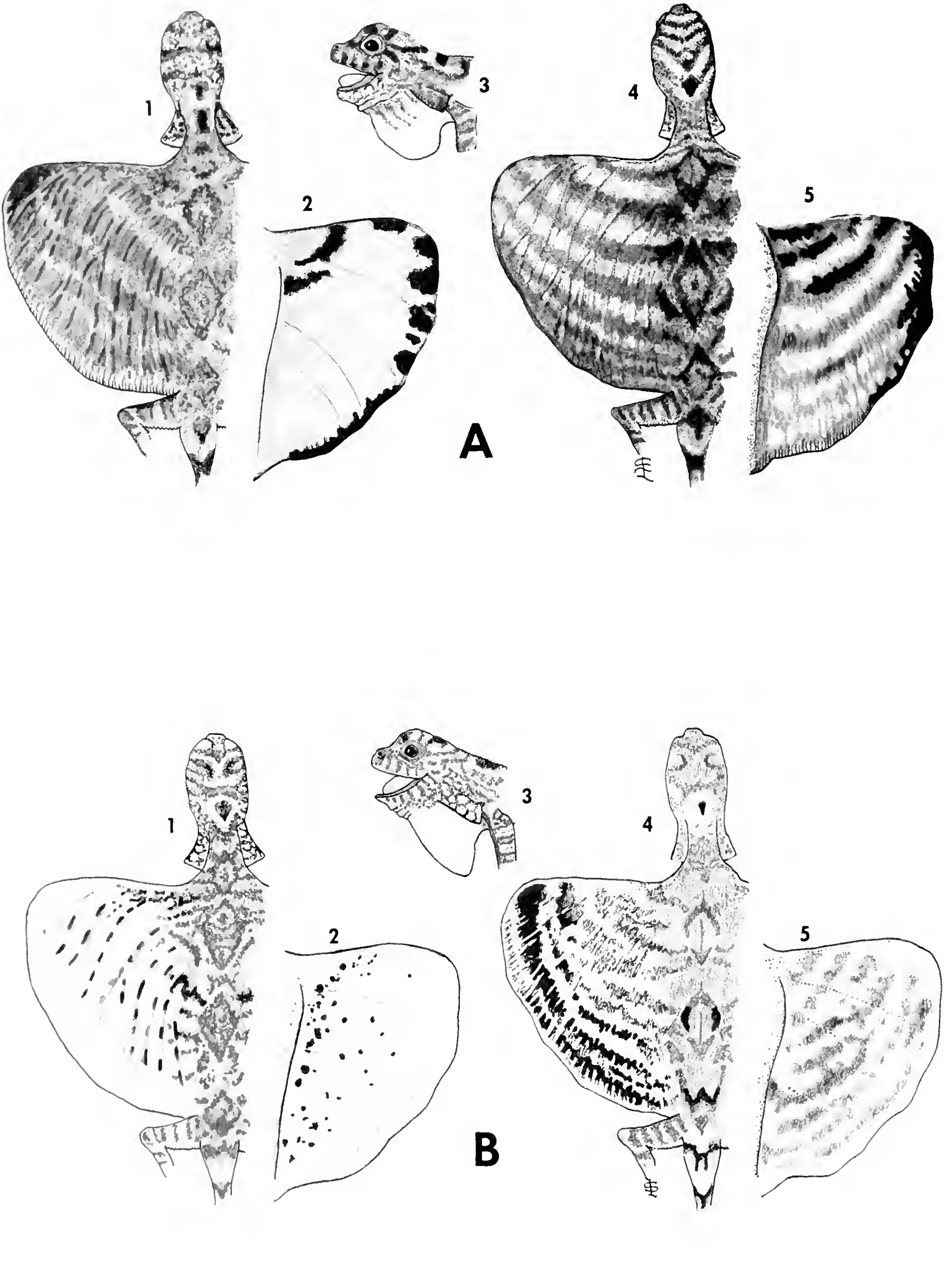
A male, MCZ 173316, from Tahuna was observed giving an apparently full display involving throat fan, lappets, and patagia while perched on a coconut palm at ca. 5 m above ground.

THE TYPHOON ISLANDS
Figure 10

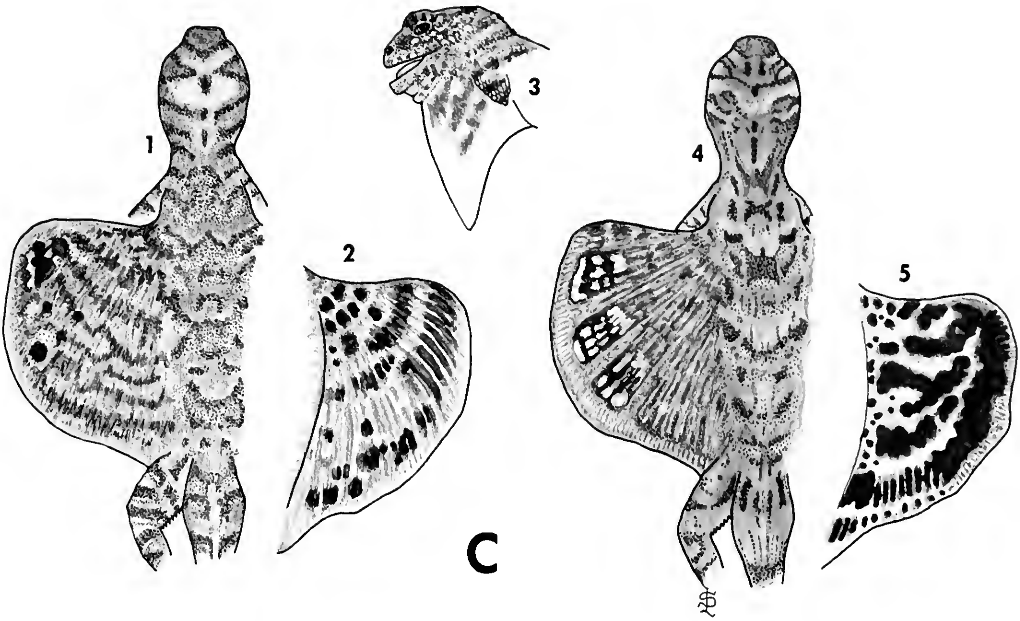
In February and March, 1988, I joined Charles A. Ross, U.S. National Museum of Natural History (USNM), in the Philippines. He reported collecting specimens of an apparently novel *Draco* in the Batanes, central in the Typhoon Island chain. I approached Dr. Henry Jarecki who not only arranged financial support for our expedition, but who enthusiastically participated in the field work on Luzon, Negros, Mindoro, and the Batanes, which resulted in garnering the fresh specimens and comparative material enabling the description of *Draco jareckii*.

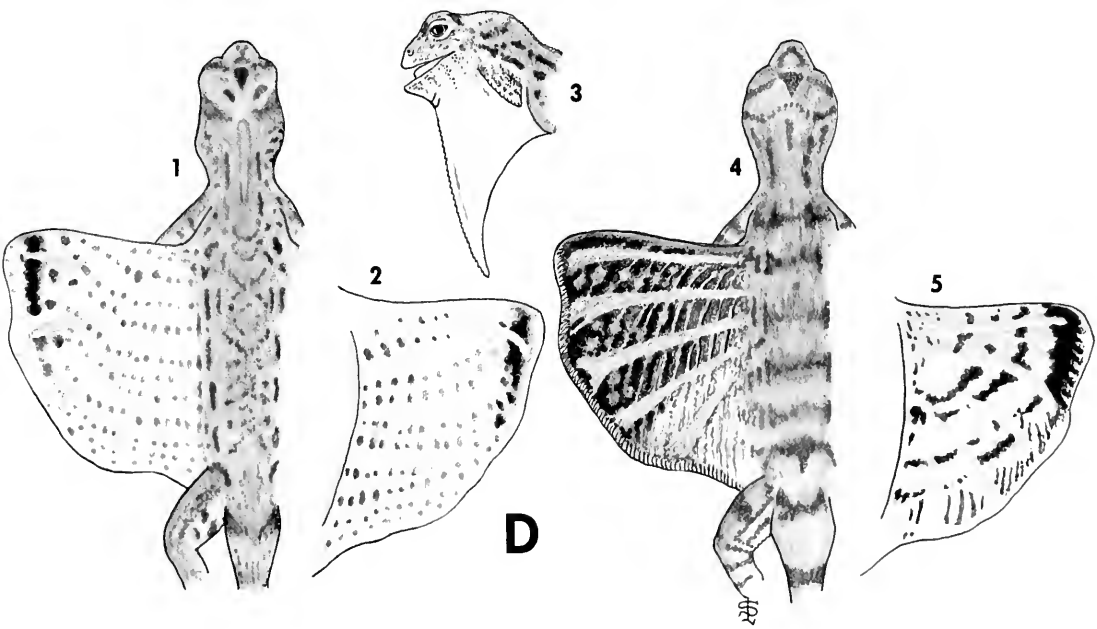
Draco jareckii sp. nov.

Type. National Museum of the Philippines (NMP) 1797, originally MCZ 173411, collected at Basco, Batan Island, Batanes Prov-



F[illegible] 8 [illegible] Draco. A, D. caerulhians, Manganıtu, Sangihe, Far Moluccas; male MCZ 173321, type; female, MCZ 1[illegible] [illegible]notus, Aırmadıdı, Sulawesi; male MCZ 173352; female, MCZ 173355. C, D. jareckii, Basco, [illegible] Islan[illegible] [illegible]MP 1797 (formerly MCZ 173411), type; female, MCZ 173416, paratype. D, D. spilopterus,





Alaminos, Laguna, Luzon; male, MCZ 173352; female, MCZ 173355. In each case 1 is male, dorsal view; 2 is male patagium, ventral view; 3 is male head; 4 is female, dorsal view; and 5 is female patagium, ventral view.

ince, Philippines, 11 March, 1988, by J. Lazell. Figure 8.

Type-Locality. Figures 10 and 11.

Paratypes. A total of 28 from Batan Island: MCZ 44142-4, 173412-6, and U.S. National Museum (USNM) 266500-13, Basco and north and east of Basco, up to 3 km. MCZ 173405-6, 173410, Ivana. MCZ 173408, Sitio Diptan. MCZ 173409, Imnajbu. MCZ 173404, Sitio Nacamaya.

Diagnosis. A *Draco* of moderate size, 67–90 mm SVL in both sexes. Patagia reduced, the greatest lateral width of a patagium 25–30% (av. 28 ± 1.6%) SVL. Five patagial ribs. No tympanum. In STD, 9–12 (av. 11 ± 0.9) keeled middorsals, 13–16 (av. 15 ± 0.8) keeled midventrals, 14–20 (av. 17 ± 1.7) oculotemporals, and 13–19 (av. 16 ± 1.7) midnuchal crest scales. There are 13–18 (av. 15 ± 1.2) paired, cristate midcaudals. There are 6–8 (av. 7 ± 1.0) postrostrals. The patagia in both sexes are largely dark, patterned in shades of gray.

Description of the Type. An adult male 76 mm SVL, tail 127 mm, and STD 8.9 mm (12% of SVL). The greatest width of the patagium, measured from the lateral chest, is 23 mm, 30% of SVL. The rostral is tiny, scarcely larger than the seven scales which border it.

There are 11 sharply keeled to mucronate middorsals, 14 strongly keeled to tectiform midventrals, and 15 oculotemporals in STD. Enlarged, mucronate basipatagials, interrupted by undifferentiated scales, form a cristate line; the minimum STD count made of contiguous scales in this series (including some undifferentiated small ones) is 13.

The midnuchal crest is prominent, consisting of spike- or blade-like tectiform scales anteriorly; there are 16 in STD.

Enlarged spike-like scales, interrupted by undifferentiated granules, form a cristate lateral nuchal line; the minimum STD count of contiguous scales is 21. There are scattered tubercular or spike-like scales on the sides of the head and neck, but no supraciliary thorn.

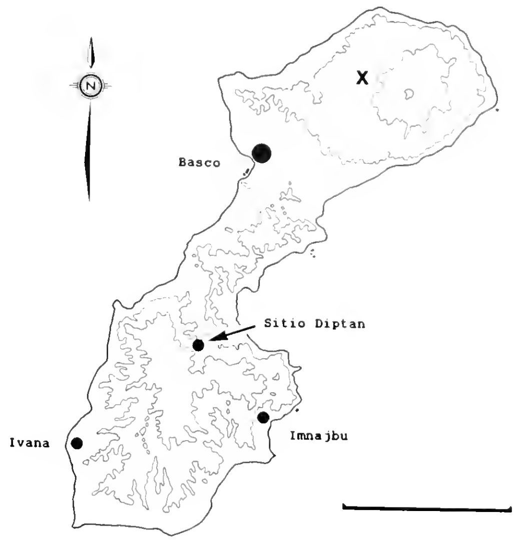


Figure 11. Batan, Batanes, Typhoon Islands. Contours are at 100, 500, and 1,000 m. Localities for *Draco jareckii* are dotted. X marks Sitio Nacamaya. Bar, lower right, is 5 km.

There are notably enlarged longitudinal scale rows on the tail. The most prominently cristate are the paired middorsal caudals (midcaudals); 15 pairs of these are contained in the length of the extended lower leg.

There are 28 subdigital lamellae under the fourth toe, counting from its plantar separation.

In life the type was patterned largely in shades of gray-brown dorsally. Dull fawn brown on the head and anterior trunk was broken by sooty to slate-gray brown tones, especially posteriorly. On mid-trunk and tail, brown gives way to shades of lead to ashy gray with a greenish tint posteriorly. Laterally the head was patterned in ash-gray and warm brown, shading to yellowish on the upper eyelid.

The throat fan is moderately long, bladelike, and was lemon yellow with a beige-pink tip and gray marbling basally. The 22 mm fan is 29% of SVL and 138% of head length.

The lappets are clothed in large tectiform scales dorsally and were not distinctively col-

ored. Ventrally, however, they bear smaller scales and were pale yellowish-gray with dark gray mottling.

The belly was near-white with a faint yellow cast laterally.

The dorsal patagium was mottled in shades of ash to slate-gray, with brown tones postero-basally, in irregularly concentric zones. The shades of gray contrast especially antero-distally. The radials are inconspicuous.

The ventral patagium is rather similar, but of a more contrasting ash and soot, roughly concentric pattern. A suffusion of yellow was discernable between the ribs posteriorly.

Color change seems very limited and involves lightening or darkening of the dorsal trunk. Gape color was not noted in *Draco jareckii*.

Male Paratypes. Because I collected living specimens all over Batan Island (Fig. 11) and detected no hint of geographic variation, I designate all specimens from that island I have examined as paratypes. These are MCZ 173405–9, 173413–4, 44142, 44144, USNM 266501–6, 266508–9, 266511, and 266513.

The smallest apparently adult male is MCZ 44144: 68 mm SVL, tail 124 mm, STD 8.3 mm (12% of SVL). A smaller male, MCZ 173407 from Ivana, 49 mm SVL, has a typically juvenile short snout.

The largest male, MCZ 173405, also from Ivana, is 90 mm SVL, tail 164 mm, STD 10.0 mm (11% of SVL).

Males have 10–12 (av. 11) middorsals, 13–16 (av. 15) midventrals, 15–20 (av. 18) oculotemporals, 12–14 (av. 14) basipatagials, and 17–21 (av. 19) lateral nuchals in STD.

There are 13–19 (av. 16) prominent middorsal nuchals anteriorly in STD.

The patagia are strikingly narrow. Their greatest widths, measured from the lateral chest, are 25–30% (av. 28%) from SVL. Two of nine adult males have broken and healed patagial ribs. MCZ 173405, the biggest male at 90 mm SVL, has two broken and healed ribs in the left patagium; MCZ 173409, 87 mm SVL, has one in the left also. One male, USNM 266505, has two holes with healed edges in the right patagium, between the second and the third ribs.

The throat fans are of moderate size for the genus: 27–31% (av. 29%) of SVL; 130–143% (av. 137%) of head length. All are blade-like, tapering to acute points.

Coloration in life is not especially variable. Topotypic Basco males MCZ 173413–4 had light yellow fans with bright pink tips. The gray on the basal portions of their throat fans was in spots not amalgamating to marbling, and paler than in the type. A male from Ivana, MCZ 173405, achieved the darkest coloration seen: chocolate brown and soot-black with golden tints reduced and present only as lateral highlights on transverse trunk markings. Another from the same locality, MCZ 173406, had a lot of golden tinting on the trunk but none on the legs. This specimen had the most pink on the throat fan.

The male from Sitio Diptan, MCZ 173408, had the palest throat fan noted, but still pale yellow with a pink tip. This specimen had mustard-color smudges on the ventral patagia.

A juvenile male from Ivana, MCZ 173407, gives evidence of the ontogeny of coloration in this species. It is 49 mm SVL. The dorsal coloration was ash and slate gray without brown tones. There was no ventral yellow. The ventral patagia, however, showed the richest yellow seen in a male. The throat fan was grayish and showed mottling of yellow and pink in the areas where these colors dominate in adults.

Female Paratypes. I regard all specimens from Batan as paratypic: I have examined MCZ 44143, 173404, 173410, 173412, 173415–6, USNM 266500, 266507, 266510, and 266512. In size and squamation the sexes are similar. Females vary: 67–90 (av. 81) mm SVL. The smallest, MCZ

173412, from Basco, has a 121 mm tail and 8.6 mm STD (13% of SVL). The largest, MCZ 173416, also from Basco, has a 175 mm tail and 12.1 STD (13% of SVL).

There are 9–12 (av. 11) middorsals, 14 or 15 (av. 15) midventrals, 14–18 (av. 16) oculotemporals, 10–14 (av. 13) basipatagials, and 17–23 (av. 20) lateral nuchals in STD.

The midnuchal crest is well developed. There are 15–18 (av. 17) spike-like, testiform midnuchals anteriorly in STD.

There are 13–16 (av. 15) pairs of enlarged, cristate midcaudals. There are 27–30 (av. 28) subdigital lamellae under the fourth toe counted from its plantar separation.

The patagia are strikingly reduced. The greatest width of the patagia, measured from the lateral chest, is 26–30% (av. 28%) of SVL.

In life female coloration averaged darker, grayer, and less brown than male. Females often showed more golden-yellow tints on the head, dorsal trunk, and limbs. The throat fan is tiny, obtuse, and was pale yellow with sooty spots. The lappets were washed with yellow ventrally.

The dorsal patagia in life were darker than in males with a different pattern. A slatey to sooty intercostate pattern contained bold, near-white and gray-greenish blotches. There were prominent light, ash to lead gray radials. There was a brown tinge postero-basally.

The ventral patagia were more boldly marked than in males, approaching black and white with a considerable yellow or yellowish-green postero-basal wash.

Of note is MCZ 173410 from Ivana, which showed the most yellow-gold tints seen in the species. This coloration was on the scale bases; the scale edges were gray. The yellow-gold tints were especially prominent as posterolateral components of the transverse markings on head, trunk, limbs, and even dorsal surfaces of the feet.

The only specimen taken in wet forest, on the west slope of Mount Iraya at Sitio Nacamaya, MCZ 173404, was not unusually colored. This is described in my notes as having a pale beige belly, most richly colored at the vent. Her dorsal patagia were near black with a plumbeous border, gray radials, and near-white frosty patches in her intercostate pattern.

USNM Paratypes. Fourteen specimens collected by C. A. Ross and colleagues were received after this work was in press. Most were shot, sometimes more than once, often precluding diagnostic measurements and counts. In all, the pattern is very well preserved except right around damaged tissues. All have been very useful in confirming the diagnostic pattern characters of *Draco jareckii*.

There are ten males. Two, USNM 266503–4, are too damaged for either SVL, head length measurements, or nuchal crest counts. Two, USNM 266501 and 266506, cannot yield SVL but do provide fan and nuchal crest characters. One, a juvenile, USNM 266508, was not used for head or STD measurements but is usable for patagia.

Thus in six males the patagia are 25–29% (av. 27.5 ± 1.7%) of SVL. In seven males the fans are 120–146% (av. 132 ± 11.4%) of head length, as great a variation as seen in the entire species. In six males there are 12–17 (av. 14 ± 1.8) midnuchal crest scales in STD.

There are four females. One USNM, 266500, was shot through head and body, precluding measurements and counts. One, USNM 266507, was shot through the trunk, precluding an accurate SVL measurement but STD and nuchal crest are measurable. One, USNM 266510, is a tiny but nearly perfect specimen, 34 mm SVL—the smallest examined. In pattern it is a replica of the adult females.

Thus, in two females the patagia are 25 and 30% of SVL and in two there are 17 and 19 nuchal crest scales in STD.

Two virtually undamaged specimens are especially notable, retaining beautiful patterns and rich brown, gray, and blue-gray colors, when examined 7 February 1991: USNM 266512, a female 82 mm SVL, and USNM 266513, a male 77.5 mm SVL.

A topotypic adult female is shown in Figure 8.

Comparisons. The only previous author to have considered specimens Field Museum of Natural History (FMNH) 100882–3, was Inger (1983). He placed them, *D. spilopterus* of Luzon, *D. everetti* and *D. ornatus* of Mindanao, and many other easily distinguished forms in the synonomy of *Draco volans* (see Ross and Lazell, 1991). In general, Inger's (1983) species are characterized by the sorts of broad-brush, if modal, morphological trends used by many other modern systematists (not me) to diagnose genera (e.g., Malnate and Underwood, 1988, for Philippine forms; Guyer and Savage, 1986, for anoles). Inger's species may correspond to species groups, or real species in a few very geographically restricted cases. His composite making *D. volans* was untenable, as shown by Musters (1983), who at least recognized sympatric species immediately distinct in major morphological, mensurable, and meristic characters. Nevertheless, the FMNH specimens are problematical and not paratypes of *Draco jareckii.* Both are from "Batanes I," but bear no more specific data. The Batanes group includes at least 10 islands large enough to support *Draco* on at least three different banks. Batan Bank alone has four islands. These specimens are described on the FMNH printout as "part of the Edward Taylor collection," but the collector is listed as "unknown." One specimen, FMNH 10082, an adult male 81 mm SVL, may well be a *Draco jareckii.* It has reduced patagia, their width 26% of SVL, and a prominent midnuchal crest of blade-like scales, only 13 contained in STD. In all other meristic characters it fits *D. jareckii* (or *D. spilopterus*). The throat fan seems very short, possibly from loss of elasticity or shrinkage in formalin. It extends only about 20 mm, 116% of head length and 25% of SVL.

In coloration FMNH 100882 is dark and muddy, also a likely result of strong formalin. The patagia are darkly pigmented in a roughly concentric pattern consistent with *Draco jareckii.* Given the present paucity of our knowledge, I cannot guess which island this specimen may have come from.

The second specimen is the more remarkable. FMNH 100883 appears to be a typical Luzon *Draco spilopterus.* The color pattern is reasonably preserved, the patagia pale yellowish with the dark spots in roughly concentric zones picked up by the radials, as in Manila region males. The specimen is badly damaged. Notably, a deep and broad laceration crosses the anterior nuchal region. Flesh and probably scales are missing, so this diagnostic count cannot be made. The specimen is an adult male 79 mm SVL. The throat fan is shredded, the hyoid skinned. Nevertheless, what remains extends to 24 mm, 157% of head length and 30% of SVL. The patagia are broad, 34% of SVL in width. I suspect this individual indeed came from Luzon and somehow got associated with the Batanes individual. The possibility of sympatry between the two species in nature seems remote to me.

Musters (1983) recognized only a single species on Luzon, *Draco spilopterus,* and expanded its range through the Philippines to include all of the mid-sized, generalized *Draco,* however disparate in coloration, pattern, or details of squamation. Because *Draco jareckii* is the geographically extreme member of the genus yet discovered in the eastern portions of the range, it must be derived from *Draco spilopterus* or a common stock, and requires close comparison to that species on Luzon.

Draco jareckii is immediately distinct from all known members of the genus in reduction

of the patagia. Measured from the lateral chest, the patagia of all other *Draco* I have seen were at least 33% of SVL in greatest width. In 24 *D. spilopterus* from the type locality, Manila (5) and nearby central Luzon (19), the greatest width of the patagium is 33–39% (av. 36%) of SVL. The adaptive significance of this character is discussed under "ecology and behavior," below.

The male throat fan of *D. jareckii* is also reduced compared to that of *D. spilopterus*. While never longer than 30% of SVL or 142% of head length in *jareckii*, it is 33–40% (av. 37%) of SVL and 152–204% (av. 186%) of head length in *spilopterus*.

In squamation the two species are rather similar, but *D. jareckii* has a more prominent midnuchal crest. In both sexes these crest scales are relatively large, 13–19 (av. 16 ± 1.7) are contained in STD, counted from the anteriormost, obviously enlarged scale. In *D. spilopterus* the midnuchal crest is less conspicuous. In both sexes there are 20–27 (av. 24 ± 1.9) in STD.

The most spectacular distinctions between *Draco jareckii* and *D. spilopterus*, or any other Philippine *Draco* known to me, are in coloration and pattern. While at the British Museum (Natural History), I was able to compare topotypic Manila *spilopterus* directly to Wiegmann's (1835) plate 15, which serves as the type specimen. Of the series BMNH 82.8.29.72–74, an adult male, BMNH 82.8.29.73, is a near-perfect match for Weigmann's plate 15. All of these specimens, two males and a female, two males from Manila (MCZ 7768 and 170253), and two males from "near Manila" (MCZ 26173–4) are included within the range of pattern variation shown by a series of 17 collected, chronicled, and photographed alive by Ross, Jarecki, and me at Alaminos, Laguna Province, Luzon, on 4 March, 1988. This is ca. 47 km SW of the Manila.

Because *Draco spilopterus* seems never to have been depicted in life, I include both sexes in Figure 8. Even Taylor (1922) gave only a brief description of the male in life (and females only as preserved).

In life, adult males from Alaminos (MCZ 173451, 173453–4, 173456–7, 173460–1, 173464–5) were dorsally patterned in brown. They were warm, light, fawn brown on the napes, darker posteriorly, and with dark gray-brown transverse markings. Ventrally they were palest gray-green, nearly white. Their throat fans were brilliant yellow, shading to pink distally; the brightest pink was along the antero-distal fan edge.

The male dorsal patagia were bright yellow, shading rather abruptly through orange to red or orange-red along their bases. There was narrow costate pattern of gray-brown, especially distally along ribs two and three. There were boldly contrasting brown or gray-brown spots which appeared rather randomly scattered over the patagia. In some specimens these spots tended to form 8 to 10 roughly concentric sets. These spots often coincided with radials, and the radials may carry brown scales for varying distances. These spots amalgamated to form an anterodistal bracket.

The male patagia ventrally were paler with the spots showing through. The bracket was intensified, slate to sooty, and may overlay the costate pattern. The sides of the trunk along the patagia were blue-green.

In life, adult females (MCZ 173455, 173458, 173462–3, 173466–7) were duller than the males, conspicuously lacking the blue-green sides, orange or orange-red dorsal patagial bases, and bright yellow dominant dorsal patagial coloration.

Dorsally the female patagia showed a costate pattern of light gray-brown on a ground of dark gray-brown and slate. There was a yellow wash posteriorly and distally.

Ventrally the female patagia were little pigmented, so most of the somber dorsal coloration showed through, but paler. The posterodistal yellow was more conspicuous,

and the sooty bracket especially prominent. There were scattered sooty spots. The richest colors of females tended to be yellow tones on the otherwise drab, gray-spotted, small throat fan, and the abdomen and underside of tail.

In both sexes the patagia of *D. spilopterus* are distinct from those of *D. jareckii*, but the distinctions in females are most obvious in the amount of ventral pigmentation in *D. jareckii*.

Ecology and Behavior. Batan Island appears brutally cutover, virtually sheared bald. Except around the volcano, Mount Iraya, in the extreme northeast, there is not even remnant forest. There are only scattered trees in ravines, for shade around dwellings, and in pathetic, obviously ineffectual windbreaks straggling across the agrarian scene. It is not unusual to see several *D. jareckii* in a single tree, although it may be a long hike to the next such tree. Interestingly, this species does not seem to be more common in the forest on Mount Iraya, although regularly seen there too.

Draco jareckii regularly perch, often head down, on trunks of trees and palms at 1.5 to 6 m. This is notably lower than most *Draco* perch elsewhere in coastal zones where I am familiar with them. In part, low perch height corresponds to the battered trees, scattered hat-racks in the wind. However, many trees are tall enough for *Draco* to perch higher regularly and it is never necessary for them to perch so low. They escape by climbing up and do not show much reluctance to enter tree crowns, despite the presence of arboreal snakes on the island (but not necessarily in the trees).

We repeatedly observed male *Draco jareckii* display with throat fans and lappets, but never saw one fan the patagia. For me this truncated behavior fits into a larger pattern.

The reluctance to spread the patagia, the reduced size of the patagia, the presence of broken patagial ribs or patagial holes in about 10% of individuals, and the ubiquitous presence of *D. jareckii* in sparsely vegetated terrain suggest that a novel adaptive realm has been entered. I submit we are seeing here the reversal of the evolutionary trend which set *Draco* apart from other lizards; we are going back to a flightless *Draco*. Under the heel of hardship, brutal natural selection is operating in these blasted isles.

PREDICTIVE BIOGEOGRAPHY

A major goal of science is accurate prediction. Since the Lesser Antilles have been long studied in great depth in terms of biogeography and the evolutionary relationships of their faunas, comparison to the Far Moluccas and Typhoon Islands provides an unparalleled opportunity for complex prediction. Just how close are the similarities between these remote island realms?

The Lesser Antilles are the largest of the three archipelagos, spanning seven degrees of latitude. They spread over about 725 km north-south, and 310 km east-west. Their western arc is called the "first cycle" because its islands have not been deeply submerged and capped with oceanic limestone. St. Croix, at the northwest extreme of the westen arc, is geologically distinct from the simple volcanoes which make up the rest. The eastern arc, from Sombrero to Barbados, is the "second cycle." The volcanic foundations of these islands have been largely or completely overlain with limestone dating from perhaps the Miocene (ca. 25 million years ago), when ocean levels were much higher than today.

The Lesser Antilles are in the Trade Wind zone, where the winds blow almost incessantly from the east or northeast. This constant windstream has dramatically influenced life on the islands. There are sharp distinctions between windward and leeward; at about 650 m above sea level even the most arid land shifts abruptly to rain for-

est. All Lesser Antillean islands high enough to support rain forest are in the western arc. There are nine over 650 m, and five over 1,000 m.

One immediately wants to know how many islands are included in each archipelago. The Lesser Antilles are well-mapped, so a count is theoretically possible. But just what is an island? How high above water must it rise? How far must it be distant from other things (like boulders) protruding above the sea? The Lesser Antilles lie between the Puerto Rico Bank (north) and the continent of South America (south). There are 16 separate Lesser Antillean banks supporting islands today. The concept of "bank" is more useful than that of "island." A bank is a submarine platform whose edges correspond closely to sea level during a glacial maximum – when sea level was about 100 meters lower than it is today. Oceanic islands lie on banks disjunct from the continental shelf, which was also dry land at glacial maximum. The last glacial maximum, the Wurm, was about 70,000 to 10,000 years ago. In counting the banks of the Lesser Antilles I have not included La Blanquilla, a southwestern outlier just off the South American Shelf. It is perhaps an analog of the Nain Bank, which lies just north of Manado and the Sulawesi Shelf, or Lu Tao Bank, which lies just east of Taiwan.

Omitting Nain, the Far Moluccas also comprise 16 banks. The best maps show about 54 islands, total, but I know that count is too low because I have seen islands – large and well-vegetated – that are not mapped.

At their northeast ends both the Far Moluccas and the Lesser Antilles approach a major island on a large and complex bank. The Far Moluccas nearly reach Mindanao on the Greater Philippine Bank. This vast bank includes most of the major Philippines to and including Luzon. The closest Far Molucca Bank is Sarangani, closer to the southern tip of Mindanao than to its next nearest neighbor, Kawio, to the south. Thus, the Sarangani Bank (politically part the Philippines) is reminiscent of the St. Croix Bank in the Lesser Antilles. The Far Moluccas' tiny Miangas, away to the northeast, reminds one of the Lesser Antilles' Sombrero.

However, the comparison is not perfect. The Greater Philippine Bank is much larger and more complex than the Greater Puerto Rico Bank of the Antilles. There is no deep water channel like the Anegada Passage between the Philippines and the Far Moluccas. With lower, glacial maximum sea levels, over-water dispersal might be easier between the Philippines and the Far Moluccas than between Puerto Rico and the Lesser Antilles.

At their southern ends the comparison is even less close. The Far Moluccas approach the Sulawesi Bank, another huge oceanic island system. The Wallace Line runs through the deep water channel that separates Borneo and Palawan – continental shelf islands solidly part of the mainland at glacial maximum – from Sulawesi, an oceanic island with a depauperate, largely endemic fauna derived from a few stocks able to cross water. The Lesser Antilles approach the South American continent with its large shelf islands of Trinidad and Tobago, which are a vastly richer source for potential colonizers, but ones not pre-selected for over-water dispersal.

The Far Moluccas span about four degrees of latitude, from just below 2°N to just below 6°N. That is about 405 km, or 56% of the linear distance of the Lesser Antilles. Linear north-south distance is what over-water dispersing animals must cross to colonize the islands. At 262 km wide, east to west, the Far Moluccas are better than 80% of the width of the Lesser Antilles. This provides a good, broad spread for dispersers to hit.

I do not have the sort of richly detailed, comprehensive geological evidence available for the Far Moluccas that I had for the Lesser Antilles. However, Hamilton

(1979:191–197) provides a historical scenario and some specific data for the Sangihe, Talaud, and Nenusa Banks. The western arc or Sangihe Ridge is said to be of Miocene age with numerous active to barely dormant volcanoes along it, quite like the first cycle of the Lesser Antilles. Sangihe itself is said to be all Quaternary igneous extrusives on the surface. The land areas on Sangihe Ridge are the subaerial extensions of the volcanic region of northern Minahasa, Sulawesi.

The large islands of the Talaud Bank are older, like the eastern, second cycle islands of the Lesser Antilles. Hamilton (1979) describes them as a "polymict melange" of "broken formations" of Tertiary age. He notes extrusives such as basalt and sedimentary formations trending towards metamorphosis such as clay, shale, sandstone, and chert. In keeping with their greater age (and in congruity with the Lesser Antilles) these eastern arc islands are lower than the younger western arc; the highest peak on Karakelong—largest of the group—is a mere 660 meters. The Talaud Bank is geologically kin to the San Agustin Peninsula east of Davao Gulf, southeastern Mindanao.

Interestingly, Hamilton (1979) describes the Nenusa Bank islands, geographically intermediate between the Tertiary lands of Talaud and San Agustin, as Quaternary and entirely sedimentary: "raised reefs" on "marl and sandstone." There are Lesser Antillean islands with only oceanic limestone at their surfaces: Anguilla, Sombrero, and Barbuda. These islands are also in the northwest of their archipelago. How much further one might carry geological analogy to the first and second cycle generic sorts of Lesser Antillean islands is presently unknown to me.

There is no arc-joining bank in the Far Moluccas corresponding to the Guadeloupe Bank of the Lesser Antilles. However, the large and complex Sangihe Bank offers tempting parallels. Sangihe itself, like La Guadeloupe, is a high island for its entire archipelago: 1,320 m versus 1,354 m, respectively.

Sangihe and La Guadeloupe are just about the same area, too. Both are attended by several lower islands that would unite with them at glacial maximum. The largest island in the Far Moluccas, Karakelong of Talaud, is at least as big as Martinique, largest of the Lesser Antilles (note that the two parts of Guadeloupe—La Guadeloupe proper and Grande Terre—are actually separated by sea water today). However, Karakelong is very low compared to 1,397 m Martinique. Also, the Talaud Bank is a complex of large islands; Martinique has only tiny coastal cays on its bank.

The resemblance of Sangihe to Martinique is striking. Both have a high northern massif, 1,320 m and 1,397 m respectively. Both have low peninsulas south and east. Because these peninsulas break up into islands during interglacials (as at present) on Sangihe, there may be chances for a combination of relatively weak ecotypic selection to combine with isolation and produce distinctive subspecies on the Sangihe Bank.

As noted above, one striking difference between the Far Moluccas and Lesser Antilles results from their positions relative to the equator. Both are tropical archipelagos, but the Far Moluccas are so close to the equator as to be in the equatorial doldrums: there is little breeze. The Lesser Antilles are far enough north to be plied by the trades. The lowlands of the Lesser Antilles are dried by the ceaseless winds; the highlands, above 650 m, are soaked by frequent rains and cumulus clouds carried by the winds; the largest islands have dramatic ecological zones: rain forests high and to windward, desert rain shadows to leeward. Ecological zonation will be weak in the Far Moluccas.

To date we know far less about the animal life of the Far Moluccas than we did of the Lesser Antilles in 1920. A few ornithologists and entomologists (or at least professional

collectors representing those disciplines) have visited the larger islands of Sangihe and Talaud. I may have been the first herpetologist to ever visit the Far Moluccas. In 1986 I went north from Manado by small boat only as far as Biaro (Lazell, 1987b), and in 1988 flew north to Sangihe.

There are 17 separate island forms of *Anolis* in the Lesser Antilles. There are 19 other intergrading, ecological subspecies on those big islands with Trade Wind caused zonation; since the Far Moluccas lack such zonation it seems unfair to include them in a comparison. The 17 forms tend to be exclusive on individual banks, but five banks (Anguilla, St. Kitts, Antigua, St. Vincent, and Grenada) each have two full species. The Guadeloupe, Iles des Saintes, and Marie Galante Banks share one highly varied species. The northern Lesser Antilles, south through Dominica, have *Anolis* of Greater Antillean origin. The southern islands, north through Martinique, have *Anolis* of South American origin. As one might predict, *Draco biaro* is most closely related to Sulawesi forms (Lazell, 1987a).

There are three roughly distinguishable ecomorphs of Lesser Antillean *Anolis:* generalized trunk perchers, big tree giants, and rock and brush dwarfs. Few generalized trunk perchers attain large size. Of eleven species, only three—*nubilus*, *oculatus*, and nominate *marmoratus*—regularly exceed 80 mm SVL. Only one subspecies, *Anolis marmoratus ferreus*, reaches giant size, exceeding 100 mm SVL. Most generalized trunk perchers live alone, without sympatric congeners. Two however, *trinitatis* and *aeneus*, occur with big tree giants. One, *gingivinus*, is sympatric with a rock and brush dwarf.

No analog of rock and brush dwarf *Anolis* has ever been found in *Draco*, the flying lizards. Indeed, their lifestyles call for gliding, which in turn requires relatively high perches like tree trunks. I discount rock and brush dwarf *Anolis* from my predictive comparisons. I believe *Draco* are the analogs of generalized trunk perching and big tree giant *Anolis*.

Much of the diversity at subspecies level in Lesser Antillean *Anolis* derives from the striking ecological zonation of the highest islands. This sort of zonation is reduced or absent from the Far Moluccas and Typhoon Islands for meteorological reasons. Eliminating ecological zone subspecies dramatically reduces the number of kinds of *Draco* I must predict for the Asian archipelagos if the notion of *Anolis* analogy is correct.

In the Lesser Antilles there are a total of eleven species of generalized trunk perchers. All but two, *Anolis marmoratus* and *A. gingivinus*, are endemic to a single Bank. *A. marmoratus* occupies three banks, but two are close satellites of the much larger third. *A. gingivinus* occupies one large bank and its tiny satellite. There are three species of big tree giants. One, *Anolis bimaculatus*, occupies two banks. The others are endemic to single banks. One bank, Saba, harbors only a rock and brush dwarf.

There are 16 Lesser Antillean banks. Of these, 14, or 88%, harbor *Anolis* that might have *Draco* analogs. Only two, 12%, harbor two relevant sympatric species. One striking fact about *Anolis* sympatry in the Lesser Antilles is that it never naturally involves a member from each of the two colonizing groups. The South American group invaded as far north as Martinique. The Greater Antillean group invaded as far south as Dominica. They do not overlap. All five cases of Lesser Antillean sympatry on any bank involve a second invasion by a close relative or the same ancestral stock. Since I discount rock and brush dwarf anoles as *Draco* analogs, only two Lesser Antillean Banks have relevant sympatry, the two southernmost, Grenada and St. Vincent.

Colonizers may enter the Far Moluccas too from both north and south. We have seen that Sulawesi derivatives reach at least as far

north as Sangihe. Sulawesi has far fewer species, however, than Mindanao. Only one, *D. spilonotus,* is certainly known from Minahasa, the northern peninsula of Sulawesi. Even if the different sorts I have found there (and tacitly assume to be geographic variants of one species) prove distinct at species level, the result would still be half the number demonstrably sympatric on Mindanao (*mindanensis, bimaculatus, ornatus,* and *everetti:* Ross and Lazell, 1991; Taylor, 1922).

I predict that the shorter distances in the Far Moluccas will have facilitated independent colonizations, but the very low banks and tiny islets on three of the northernmost five will preclude sympatry on them: Miangas (Palmas), Kawio, and Nenusa.

Thus I predict two species sympatric on the other two northernmost Banks: Sarangani and Talaud. Sarangani Bank, however, is so close to Mindanao that little opportunity for full species differentiation will have occurred: colonizations will have been too frequent.

I predict the two Sarangani forms will be subspecifically related to Mindanao, Philippines species, therefore less distinct than the single St. Croix (Lesser Antillean) *Anolis* is from its Puerto Rico Bank (Greater Antillean) relatives. One Sarangani species will, I predict, be a giant (greater than 100 mm SVL.)

I predict that, because of the short distances involved, Sulawesi and Philippine *Draco* stocks will overlap in sympatry, fully evolved as endemic species, on the one other bank with two species: Talaud. One Talaud species will, I predict, be a giant.

Because the Lesser Antilles' 17 relevant forms are in 14 full species spread over a linear (travel) distance 44% larger than the Far Moluccas, I predict the *Draco* forms will not be as well differentiated. Because Far Moluccas' travel distances are shorter, colonizations and genetic interchanges will have been more frequent. Thus, I predict as many recognizable forms (subspecies as well as full species) – 17 – but only 56% as many full species: eight.

I predict full species on the Miangas (Palmas), Kawio, and Nenusa banks. I predict two more species on Talaud. I have already described *D. biaro* and *D. caerulhians;* I predict they will divide the banks between Kawio and Biaro that support *Draco.* I predict only one of the three, small, western, single islet banks will support a *Draco,* even as Aves and Saba support no relevant *Anolis,* but little Redonda does. I will not guess which one.

Two of the nine remaining subspecifically differentiated forms will, I predict, be the Sarangani Bank derivatives of Mindanao. I realize these are predicted by me to be distinct at species level from all other Far Moluccas forms, but I count them at the postulated rank of subspecies herein because they may not be endemic at species level to the Far Moluccas.

Four of the remaining subspecies I predict will be derivatives of *Draco caerulhians* on Sangihe and satellite banks. The other three I predict will be derivatives of *Draco biaro* on the three southernmost banks.

The Typhoon Islands are the smallest archipelago. They span a little more than three degrees of latitude from 19°10'N to 22°N, a distance of ca. 390 km. They are about 120 km wide, east to west. They are rather like the Lesser Antilles or Far Moluccas viewed upside-down (Fig. 2). When viewed as we normally do, their oldest (equals lowest) components are on the westernmost Bank, Fuga (four islands). The highest elevation on this bank is only 290 m, on Dalupiri. The next bank north in the western group, Calayan, is only 517 m high.

The eastern line of the Typhoon Islands, from Camiguin Norte to Lanyu (and Lu Tao), resembles the western lines of the Lesser Antilles and Far Moluccas, but is lower. The highest peaks, obvious volcanic

cones, are 1,088 m on Babuyan and 1,009 m on Batan. There has been very recent volcanic activity in this chain, for example at Didicas, just northeast of Camiguin Norte (Gonzales, 1966, p. 85).

It is difficult to guess the real number of banks. Maps available to me show a 200 m submarine contour; a 100 m contour would be far more useful. Even using 200 m, there is disagreement. A Bartholomew map of 1985 shows 11 banks; a National Geographic map of 1986 shows 12. The discrepancies involve the satellite isles of Itbayat. Are the northern islets of Mabudis and Siayan on their own, separate bank? It may not matter here, because I believe they are too small and remote to support *Draco*. Of greater concern is the great volcanic spire of Diogo or Dinem, just east of Itbayat, discussed below.

There are no *Draco* on Taiwan or in southeast China, so colonization can only have come up from the Philippines proper into the Typhoon Islands. These islands are all rather steep, with narrow banks, and therefore presented scarcely larger targets at glacial maximum than they do now. We can believe that no *Draco* has penetrated as far north as Lanyu because this island has been well studied herpetologically by Ota (1987, and references therein) and visited by C.A. Ross (pers. comm.). However, we know *Draco jareckii* exists on Batan, about 60% of the way up the chain.

I predict that lack of colonization from the north, combined with only one known parent species on Luzon (*D. spilopterus*) will limit the possibilities for species presence in the Typhoon Islands. I believe their situation is similar to the northern Lesser Antilles. None of these banks, populated by species derived from the Puerto Rico Bank (the analog in this case of Luzon), supports more than one species of relevant *Anolis* (I discount *Anolis sabanus* and the *A. wattsi* complex as irrelevant rock and brush dwarfs).

I predict only six banks in the Typhoon Islands will support *Draco*, from south to north: Camiguin Norte, Fuga, Calayan, Babuyan, Batan, and Itbayat. I believe five banks will each harbor a single full species, all five distinct from each other and as distinct from Luzon *D. spilopterus* as St. Croix *Anolis acutus* is from any Puerto Rican species. The difficulties of colonization in the Typhoon Islands will, I predict, have provided ample isolation for speciation despite the small distances between banks.

On the six comparable, proximate Lesser Antillean banks – St. Croix, Sombrero, Anguilla, St. Kitts, Antiqua, and Redonda – there are two cases of species occupying different banks: *A. gingivinus* on Sombrero and Anguilla; *A. bimaculatus* on St. Kitts and Antigua. Only the latter are subspecifically distinguishable. Even if one substitutes Montserrat for tiny Sombrero or Redonda, there are still a maximum of five full species – one with two subspecies. I believe this pattern will hold for the Typhoon Islands: five full species, one with two subspecies, on six banks.

The most intriguing area for prediction, I believe, offered by the Typhoon Islands derives from the evolution towards flightlessness described for *Draco jareckii*. I predict that patagial, gliding, and display reduction will reach their extreme on the Itbayat Bank.

Itbayat itself is low, ca. 280 m at the highest point, but entirely flanked by sheer cliffs 30 m high (Gonzales, 1966, p. 6). I could rarely glimpse it across the tumultuous sea from Batan, but neighboring Diogo (called Dinem in the Batanes) is a grand cone towering 513 m and clearly visible. These must surely be the most awful lands on Earth inhabitable for an aerial lizard, yet I believe one will be found there.

Glacial maximum sea level drop will, I predict, have provided relief from cruel selection against patagia on the Itbayat Bank. In contrast, interglacial sea level rise will have been a grim reaper indeed. Contemplating

Diogo from Batan. I could imagine Draco stranded there repeatedly by sea level rise. The opportunity to survive anti-patagial selection will have followed each glacial maximum. Should the process ever have succeeded, a cliff dwelling *Draco*, perhaps reminiscent of *Anolis agassizi* on far Malpelo in the eastern Pacific, might well be the result. I predict it would succeed upon recolonization of main Itbayat just as I envision dry island *Anolis* succeeding in invading main Jamaica following interglacials (Lazell, 1966).

Some of my predictions, above, are certain to come true. I have already examined two specimens of *Draco* from Camiguin Norte in the Typhoon Islands, in USNM, with color photographs, and they are wonderfully distinct from any described form.

If any significant number of my predictions prove true, if I have predicted even the broad outlines and approximate levels of differentiation and diversity, I will be discomfitted. A half century of observing and hunting animals has yielded no picture of the order of nature—quite the opposite. The nature I know is as chaotic as the constraints of physics allow. Nature appears to me to sidestep deftly Occam's razor and never follow the shortest distance between two points. I see grave uncertainty conspicuously perched on every tree. So far, my pursuit of *Draco* has been a remarkable and exuberating repeat of my experiences earlier on the opposite side of the Earth. If, however, I never find another new species of Draco on these islands where I predict them, I cannot be disappointed. I will not find empty archipelagos.

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